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WHITE-CRESTED COQUETTE *(Paphosia adorabilis)*

Males and female (lower), life-size, from a watercolor painting by Don R. Eckelberry.

LIFE HISTORY OF THE WHITE-CRESTED COQUETTE HUMMINGBIRD

ALEXANDER F. SKUTCH

AT the end of October 1936, the *Inga* trees that shaded the small coffee groves in the narrow valley of the Río Buena Vista in southern Costa Rica flowered profusely. The fluffy stamen-clusters of the spreading leguminous trees attracted many hummingbirds of several kinds, among which I glimpsed a crested species new to me. Hoping for a better view of this exciting stranger, I watched in the grove on a sunny morning when the hummingbirds were very active; but to my great exasperation, every time the plumed bird came in sight one of the larger kinds drove him away. Finally, I discovered that after each round of visits to the *Inga* flowers he returned to rest and preen on the same exposed twig of a coffee bush, only five feet above the ground. Here on his favorite perch he permitted me to examine him within arm's length at my leisure. Never before had I met a hummingbird at once so ornate, so small, and so confiding.

I had no difficulty in identifying him as a White-crested Coquette (*Paphosia adorabilis*). In the same coffee grove were a number of females of the same species, and a young male just beginning to acquire the adult plumage.

The White-crested Coquette has a restricted range from central Costa Rica to western Panamá. It appears to be confined to the Pacific slope except in central Costa Rica, where the low continental divide permits it to cross to the Caribbean slope, on which it has been found around 3,000 feet above sea level. Its altitudinal range is from about 1,000 to 4,000 feet. If it enters the forest, it evidently remains high in the treetops where it is rarely noticed. I have seen few of these readily identified hummingbirds except where there is a profuse display of flowers attractive to them. Among these are the *Inga* trees planted as shade for the coffee, as already mentioned. Near the plantation where I met my first adult male was another small grove where, in early November, I found a number of others, some of whom were scarcely less confiding. During the years when I had a hedge of *Stachytarpheta* along two sides of my dooryard, many Coquettes came, along with a multitude of other hummingbirds, to sip nectar from the small purple flowers of this straggling shrub of the verbena family.

At this hedge I recorded males in full breeding plumage chiefly from August to March. Males in various stages intermediate between the juvenal plumage, which resembles that of the female, and the ornate nuptial attire were seen from late May to the beginning of October. I hesitate to conclude from these observations that the males lose their head plumes and go into "eclipse" after the breeding season. Since, as in many other hummingbirds,

the Coquettes appear to wander widely in search of plants that blossom profusely, it may be that the adult males went elsewhere from mid-March to late August, in which five-month interval I recorded only one at my house, in June; although females and males in transitional plumage were present in this period, and females visited the *Stachytarpheta* throughout the year.

COURTSHIP

Toward the end of October, I watched a male Coquette in full regalia display to a female who rested on a low, slender twig close by the flowering hedge. Hovering in front of her, he oscillated rapidly from side to side, in a most peculiar lateral flight such as only hummingbirds, of all feathered creatures, appear to be capable of performing. Always keeping his breast toward the quiescent female, he swung now toward his left wing and now toward his right, alternating his direction with surprising swiftness. The length of his sideward swing between the opposite turning points seemed not to exceed one foot. The female always kept her bill pointed directly toward the displaying male. Soon she rose slowly above her perch, hovering on wing as only a hummingbird can; and he continued to float in front of her, now oscillating more slowly than before. A few seconds later they separated.

At the end of April, when the only Coquettes at the hedge were in female attire without head plumes, one of these unornamented individuals perched on a *Stachytarpheta* bush, while another, equally plain, hovered in the air, facing it, a few inches away. After this had continued for less than a minute, the first hummingbird left its perch and slowly rose into the air; and the one that had been hovering ascended with it, still facing it, and now began to oscillate rapidly from side to side, in a movement with an amplitude of only a few inches. After a few seconds, the display ended and the birds flew off in different directions. This performance resembled that of the adult male that I had earlier watched, but the lateral oscillation was shorter and less regular. I wondered whether the performer was an adult male in eclipse plumage or an immature individual.

Although hummingbirds of many kinds sing persistently and more or less melodiously from stations where they are to be found day after day in the breeding season, I have not discovered the White-crested Coquette behaving in this way.

NEST AND EGGS

On our farm at Quizarrá, in the basin of El General at about 2,500 feet above sea level, I have seen four nests of the White-crested Coquette. Two of these nests held eggs at the beginning of January and had evidently been built in the preceding month. In another nest the eggs hatched about 5 February and the young flew at the end of the month. The latest nest held eggs at the

end of February, and in early March they were deserted. These few records indicate that this hummingbird, like a number of other species, breeds early in the dry season, when flowers are abundant. The latest nest was apparently abandoned because of the increasing dryness and paucity of blossoms.

The highest of these four nests was situated about 60 feet up in a dead tree at the forest's edge. A dying orchid plant hung below a mossy branch of this tree, and to the upper side of a slender stem of the orchid the nest was attached. The other three nests were in guava trees (*Psidium guajava*) growing near our house, at heights of about 16 to 21 feet above the ground. They were built upon slender twigs far out from the trunk, where they were only slightly shaded and screened by the terminal foliage and would have been conspicuous if they had not been so small. One nest was placed in an open V-shaped crotch. Another was supported at its base by a thin lateral twig, but its upper portion was quite unattached. Each nest was a tiny open chalice of downy materials, well covered on the outside with gray or greenish gray foliaceous lichens.

The contents of the three low nests could be seen in a mirror raised on a long pole. Each of them contained two minute white eggs when they were found.

INCUBATION

Nest 2 was situated close by the house, where it could be conveniently watched from a window. On 30 January 1947, when the incubation period was drawing to an end, I watched from 5:35 to 11:35 AM, and on the following day my vigil extended from 11:52 AM until 5:30 PM, when the light was growing dim. The morning of 30 January was sunny and cool, and the afternoon of 31 January was lightly clouded, with intermittent sunshine. Only the female attended the nest, and I saw no male of the species in the vicinity. In nearly 12 hours of watching, I timed 38 sessions on the eggs, ranging from about 1 to 34 minutes and averaging 10.4 minutes. There were 39 recesses ranging from less than 1 to 23 minutes and averaging 7.1 minutes. The female Coquette spent 59.4 per cent of the day on her nest.

In the morning the hummingbird was more active than in the afternoon, and both her sessions and recesses averaged shorter. Her 23 sessions in the forenoon averaged 9.5 minutes, whereas her 15 sessions in the afternoon averaged 11.9 minutes. Her 23 recesses before noon averaged 6 minutes and her 16 recesses after noon averaged 8.7 minutes. Although she came and went more often in the morning than in the afternoon, the range of her sessions and absences was nearly the same in both parts of the day. In both the forenoon and the afternoon she took one session that lasted 34 minutes. Her longest absence in the morning was 23 minutes and her longest in the afternoon was 22 minutes. In both parts of the day, her shortest sessions, like her shortest recesses, were one or two minutes.

As she approached and left the nest, the hummingbird's flight was slow and irregular, with short advances separated by momentary pauses, when she hovered on wings vibrating too rapidly to be visible, and much jerky up-and-down movement caused by raising and lowering her tail. Like other incubating hummingbirds, she often brought material to add to her nest. Between 6:30 and 7:45 AM, she brought nine small pieces of lichen or similar material, which she stuck to the outside of the cup, although it was already so well covered that there seemed not to be space for another piece. After 7:45, I could detect nothing in her bill as she returned, but the way she wiped her bill over the outside of the nest after settling in it suggested that she had brought cobweb and was spreading it over the outer surface. She continued this until 1:25 in the afternoon.

A Snowy-breasted Hummingbird (*Amazilia edward*) often came to rest in the nest tree, which appeared to be his preferred station. Whenever he ventured close to the nest, the much smaller Coquette chased him away without much difficulty. Apparently maternal solicitude gave her the force to drive off this larger and rather aggressive hummingbird. In the coffee grove where I found my first male White-crested Coquette, the Snowy-breasted Hummingbirds were numerous and often chased the Coquettes from the white flowers of the *Inga* trees. Once a Snowy-breasted darted up and struck a perching Coquette with his breast, but the latter did not even shift his position on the twig.

On 7 January 1955, my wife and I, watching by turns, made a continuous record of activities at Nest 4 from 5:25 AM until 5:40 PM. The morning was brilliantly clear; but after noon clouds began to gather and soon the sky was almost wholly overcast, although no rain fell during the day. The female hummingbird alone attended her two eggs, taking 37 sessions which ranged from less than 1 to 78 minutes and averaged 13.4 minutes. Her 38 recesses varied in length from less than 1 to 22 minutes and averaged 5.7 minutes. She incubated with the high constancy of 70.2 per cent. Her attentiveness, however, fluctuated considerably with the time of day and was especially low between 8:00 and 10:00 AM, when she devoted much time to the nest itself, sometimes sitting for a minute or even less, flying off to search for material, then returning in a minute or so to add it to her structure. Her 30 sessions before noon averaged only 8 minutes in length and her 31 recesses averaged 4.7 minutes. In striking contrast to this, her seven sessions after noon averaged 36.1 minutes and her seven recesses averaged 10 minutes.

In the hour and a half between 8:30 and 10:00 AM, this hummingbird seemed to bring something to her nest at least 11 times. Although once she came with a tuft of seed down almost as big as herself, most of the material was in small pieces, and usually it was invisible to us. But frequently when

we could detect nothing in her bill, after settling in the nest she bent over and rubbed her bill carefully over the outer surface, evidently applying cobweb. As she did this, she spread her wings over the nest's rim. At other times she seemed to knead the material in the bottom of the cup with her feet. She was last seen to add cobweb at 12:50 PM, after which she gave no more attention to the nest itself and attended her eggs far more steadily.

Nest 3 was found in 1949 by Mr. Darwin E. Norby, who with Barbara Norby made a day-long record of incubation, which they have kindly summarized for me. In 12 hours they timed 49 sessions that ranged from about a quarter of a minute to 18 minutes and averaged 6 minutes. There were 51 absences that varied from three-quarters of a minute to 22 minutes and averaged 8 minutes. The eggs were covered only 42.9 per cent of the day. This abnormally low constancy suggested that the female was now, at the end of the dry month of February, having difficulty in finding enough food. A few days later the eggs were abandoned, as already told.

THE NESTLINGS

In the nest in the guava tree close beside the house, the eggs hatched on 5 February or in the following night. From 5:40 to 10:40 AM on 8 February, I watched the female hummingbird attend her two nestlings, to which she brought food 12 times in the course of five hours. Each feeding occupied from 22 to 54 seconds; but since I could see nothing of the young birds except occasionally the tip of a bill, I could learn no further details. The mother brooded for 18 periods ranging from 2 to 19 minutes and averaging 7.1 minutes. Her 17 absences lasted from 3 to 18 minutes and averaged 9.4 minutes. She was at the nest for 43.2 per cent of the five hours, including the time devoted both to feeding and brooding.

On 15 February, when the two nestlings were about ten days old, I again watched from 5:40 to 10:40 AM. Although the morning was cloudy and cool, the hummingbird did not brood after her first morning departure from the nest at 5:42 AM. She brought food to the nestlings nine times in the five hours, and on each of these visits she appeared to regurgitate several times to both of them, alternately. However, from the window I could see little of them until late in the morning, when they often raised their heads well above the nest's rim at mealtime.

By 25 February, the two nestlings, now about 20 days old, were well feathered, and I could see much of their bodies protruding above their nest's rim while I watched from the window from 5:35 to 10:35 AM. On this bright, cool morning the female did not brood. During the five hours she made 12 visits for feeding, on each of which she regurgitated to both nestlings. On some visits she fed both of them twice, alternately; but on others only one

of them was fed twice; and on yet other visits each received a single portion. When the mother regurgitated to a nestling only once, it appeared not to desire more. The young hummingbirds preened much, and from time to time they stood up in the nest and flapped their wings vigorously, an exercise which they often took just after receiving nourishment, first one and then the other.

One of these young White-crested Coquettes left the nest between dawn and 7:45 AM on 27 February, and the other took wing in my presence at 8:25 on the same morning. It appeared to sever contact with the nest quite spontaneously, and soon after leaving it was fed by its mother on a neighboring bough of the guava tree. These young hummingbirds were in the nest 21 or 22 days.

At no time was a male seen to take an interest in any of these four nests. On the morning when I found Nest 4, a male Coquette flew by it without stopping to investigate; but aside from this, none was seen in the vicinity.

SUMMARY

The White-crested Coquette is found in clearings on the Pacific slope of southern Costa Rica from about 1,000 to 4,000 feet above sea level. It is not often seen except where a profusion of flowers, such as those of *Inga* or *Stachytarpheta*, attracts a number of individuals to a plantation or dooryard. It is almost fearless of man.

Males in transitional plumage were seen from late May to October. Males in full nuptial regalia were rarely seen between March and August.

A flying male displayed before a perching female by oscillating rapidly sideward through an arc of about one foot, the while keeping his head toward her.

At about 2,500 feet above sea level in southern Costa Rica, nesting occurs in the early part of the dry season, from December through February. Three nests were built in guava trees in clearings, from 16 to 21 feet above the ground, and another was in an orchid plant hanging about 60 feet up at the forest's edge. The minute downy cup is well encrusted with grayish lichens on the outer surface.

In three instances, the set consisted of two white eggs. At these three nests, the females took attentive sessions which ranged from less than 1 to 78 minutes in length, although those in excess of half an hour were rare. Recesses lasted from less than 1 to 23 minutes. In 12 hours of observation at each nest, these three females incubated with a constancy of 59.4, 70.2, and 42.9 per cent; but the last was apparently losing interest, for a few days later her eggs were abandoned. In the morning, the incubating females brought much new material to their nests.

In the first five hours of the morning, one female brought food to her two nestlings 12 times when they were about three days old, 9 times when they were about ten days old, and 12 times when they were about twenty days old. Often she regurgitated to both nestlings twice, alternately, on a single visit. At one nest, the nestling period was 21 or 22 days.

No male was at any time seen to take an interest in nests or young.

EL QUIZARRÁ, SAN ISIDRO DEL GENERAL, COSTA RICA, 22 MARCH 1960

BREEDING BIOLOGY OF THE LEAST BITTERN

MILTON W. WELLER

THE Least Bittern (*Ixobrychus exilis*) is one of the most inconspicuous of all marsh birds. It is neither shy nor rare within its range but is merely a quiet bird which lives out of sight among marsh emergents. Observations on the species have been numerous but brief, and no detailed study of any phase of its breeding biology has been published. However, considerable data have been reported on the closely related Little Bittern (*I. minutus*) of Eurasia. The data presented here were obtained during 1958–1960 at Goose and Little Wall lakes near Jewell, Iowa, and at Trumbull and Rush lakes near Ruthven, Iowa.

Information was collected during marsh investigations sponsored by the Iowa State University Alumni Research Foundation and the National Science Foundation Teacher Research Participation Program. I am indebted to Cecil E. Spatcher and Robert A. Buckley for field assistance, to Drs. Andrew J. Meyerriecks and Ralph S. Palmer for assistance with literature, and to Dr. Meyerriecks for comments on the manuscript. Dr. Thomas Kent and Fred Kent of Iowa City, Iowa, permitted use of unpublished data.

GENERAL HABITS

Of the two North American bitterns, the Least Bittern leads a more over-water existence than does the American Bittern (*Botaurus lentiginosus*). The American Bittern usually is a shore-line wader which nests in edge emergents with the nest resting on the ground (Abbott, 1907; Vesall, 1940; and present study). The Least Bittern spends its time over deeper water where it uses emergent vegetation as "stepping-stones." It feeds on the open-water side of the emergents by clinging to the vegetation and extending its long neck (Eastwood, 1932; Sutton, 1936). Saunders (1926) reported that these small herons rarely missed their target and were constantly on the move when hunting. When alarmed, they assume the "freezing" action so characteristic of the group (Palmer, 1909; Allen, 1915), and when approached they take flight with legs dangling.

NEST SITES

Nesting usually occurs in emergent vegetation several feet in height. Of 89 nests found during the present study (Table 1), 50 nests found by Trautman (1940), and 30 nests found by Beecher (1942), most were in *Typha*, *Carex*, *Scirpus*, and plants of similar physiognomy. Occasionally, nests are found in *Phragmites* (Bent, 1926; Dillon, 1959), *Sagittaria* (Potter, 1917), and *Salix* or *Cephalanthus* stems in water (Bales, 1911; Baker, 1940; Potter, 1917; Trautman, 1940). One nest found by Provost (1947) was supported by barbed wire. A nest on the ground in weeds was reported by Roberts (1936: 192) and nests on bog or drift were found by Cooke (1881), Chapman

TABLE 1

NESTING COVER OBSERVED DURING PRESENT STUDY

Vegetation	No. nests
Typha spp.	13
Typha-Scirpus acutus	23
Typha-Scirpus fluviatilis	2
Typha-Salix	1
Scirpus acutus	14
Scirpus fluviatilis and *S. acutus*	11
Scirpus fluviatilis	15
Carex spp.	3
Phragmites communis	2
Mixture of any three above	5
Total	89

(1900), and Abbott (1907). Nests in *Salix* or Mangrove (*Rhizophora*) over ground were noted by Trautman (1940) and Howell (1932), respectively. Old nests of a Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and a White-crowned Pigeon (*Columba leucocephala*) were reported as bases for bittern nests by Roberts (1936) and Beatty (1943).

A natural clump of vegetation of the previous year usually forms the foundation for the nest. The importance of this old vegetation was shown by changes in the distribution of nests at Goose Lake in central Iowa. During 1958, considerable emergent vegetation remained in the center of the marsh after winter. The five nests found were in this cover. During the spring of 1959, a water level increase caused the loss of most of the old vegetation so that little cover existed in the center of the marsh when nesting started. All seven nests found during 1959 were in the edge vegetation, and although new and dense vegetation developed in the marsh center by the time of the second nestings, no nests were found there. These central emergents were used for feeding, however.

The nest base also is formed by bending down of new and old vegetation, and then short stems are added on top. Potter (1917) reported that "sticks" brought to a nest site among *Sagittaria* were laid in a criss-cross pattern like the spokes of a wheel (Fig. 1). Wackernagel (1950) made a similar generalization for the nest of the Little Bittern. The platform usually consists of the same species of vegetation as the base, but it may differ when floating debris is used. However, material rarely is carried more than a few feet. Bent (1926:85) mentions a nest built in "rushes" and constructed entirely of "sticks." A similar nest found during this study was constructed of willow

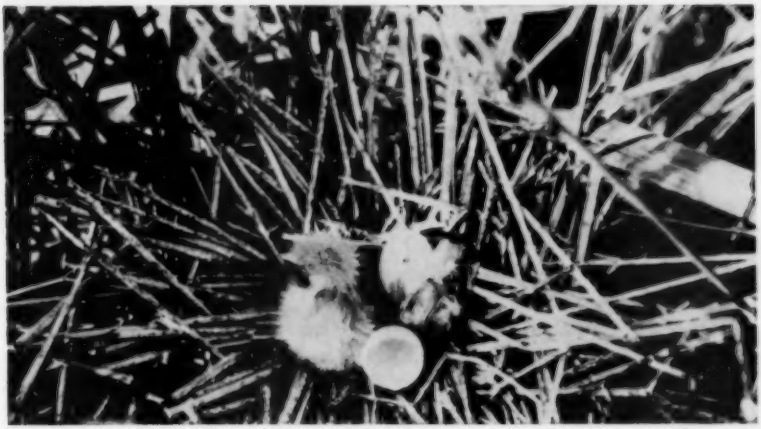

FIG. 1. Nest in hardstem bulrush at Goose Lake, Iowa, showing criss-cross pattern of nest material.

sticks, but they had been gathered from within a few feet of the nest and placed in some isolated stalks of cat-tail.

The size of the nest probably varies with the type of vegetation and the particular clump selected for the nest, but most nests are 5 to 8 inches in diameter. Bent (1904) gave measurements of two nests as 4 × 7 and 5 × 7 inches, presumably the dimensions being width and length. Simmons (1915) reported a nest 6½ inches across, and Baker (1940) found one 8 inches in diameter. A nest located by Pearson (1909) was 4 inches deep and 9 inches across.

Nests normally are placed from six up to 24 inches above water but often sink to water level from the combined weight of young and adults. Nests were found in water three to 38 inches deep; nests over land (Saunders, 1926; Roberts, 1936; Trautman, 1940) probably result from water level declines. That water conditions are important to nesting populations was shown by water level changes in Rush and Trumbull lakes in northwestern Iowa. Bitterns were common at both lakes during 1958; four nests were found in a small area of one lake and adults were seen regularly. Only one nest was found at the other lake because no intensive nest hunting was done, but the abundance of young seen in late summer indicated that numerous birds were present. In mid-May of 1959, when bitterns arrived in Iowa, water levels at both of the lakes were so low that there was little water at the base of emergent vegetation. Despite the fact that field work in the area was more intensive during 1959 than 1958, only one adult was seen at each lake and no nests or young were found.

Nests are usually located adjacent to a patch of open water, as observed not only in this study but by Cooke (1881), Simmons (1915), Saunders (1926), and Nero (1950). Of 87 nests observed for this feature in Iowa, all were 6 inches to 20 feet (averaged about 8 feet) from open water of lakes, channels, or openings made by muskrats.

PRE-LAYING ACTIVITIES

Evidence for territoriality in bitterns is limited. Kent (1951) found that nests were evenly spaced in a small lake, and observations during my study substantiate this conclusion. Relative concentrations probably develop in particularly suitable habitat. Kent (1951) found 19 nests in a 44-acre marsh, and Beecher (1942) found one nest per four acres of usable vegetation. Wood's observation (1951) of 15 nests in two acres of vegetation is exceptional. During the present study, 62 nests were found in the 83-acre Goose Lake during 1960, but some of these probably represent renests or second nests. Several cases were noted of two active nests only 15–20 feet apart. Only one observation suggests territorial behavior: Davidson (1944) saw a paired male assume a hump-shouldered defensive attitude before an intruding male. This conflict ended in the retreat of the intruder.

Nest-building seems to be performed mostly by the male. Davidson (1944) noted that at a single nest the male did most of the building although the female was present. He brought material for the female when she was on the nest. Other nest-building behavior observed later in incubation (see below) also implies that males do most of the building.

During the present study, only one nest was found prior to laying; this nest essentially was complete seven days before laying. The presence of a blind may have influenced this delay, but there is also the possibility that the nest is used as a site for courtship and copulation. No courtship display has been observed, but a "cooing" call has been described by several authors. I have never heard any such sound attributable to bitterns. Their calls have been either a coarse *gack-gack* given by birds on the nest or occasionally an *ank-ank* given by birds flushed in the marsh. However, it seems logical that the cooing call might be a courtship note given from the nest to attract females.

Copulation was witnessed at the nest twice during the present study. The first instance was two or more days after the nest was built and five or six days prior to egg-laying. In the second case, the nest held two eggs. Prior to copulation the male touched the back of the female's neck gently and preened her scapulars. Copulation on the nest during incubation is apparently common in the Little Bittern (Wackernagel, 1950; and Wijnaendts, 1954) and has also been observed in the European Bittern (*Botaurus stellaris*) by Yeates (1940).

TABLE 2

CLUTCH SIZE OF THE LEAST BITTERN (BASED ON INCUBATED OR FULL CLUTCHES)

Area	Authority	No. nests	No. eggs in clutch
Texas	Simmons (1915)	1	5
Ohio	Trautman (1940)	4	3
	Trautman (1940)	9	4
	Trautman (1940)	7	5
	Trautman (1940)	3	6
Iowa	Provost (1947)	1	4
	Provost (1947)	1	5
	Kent (1951, *in litt.*)	2	3
	Kent (1951, *in litt.*)	2	4
	Kent (1951, *in litt.*)	9	5
	Present Study	1	2
	Present Study	8	3
	Present Study	19	4
	Present Study	29	5
	Present Study	2	6
New Jersey	Potter (1917)	2	5
New York	Saunders (1926)	1	5
Ontario	Macoun and Macoun (1909)	1	5
	Macoun and Macoun (1909)	1	6
Wisconsin	Nero (1950)	1	5
Michigan	Baker (1940)	2	5
Minnesota	Roberts (1936)	4	4
Manitoba	Dillon (1959)	1	6
	Dillon (1959)	1	4
California	Moffitt (1939)	1	5
	Bancroft (1930)	1	5
	Willet and Jay (1911)	1	5
	Total	115	Mean = 4.48 ± .31

LAYING AND CLUTCH SIZE

The rate of egg-laying was reported by Trautman (1940) as one per day in four of six nests he observed. Others took slightly longer. In four nests I studied, the rate of laying was one egg per day in three nests, while another female required six days to lay five eggs. Incubation started with either the first or second egg, as indicated by embryonic development visible through a field candler. Incubation starts at the same time in the Little Bittern (Witherby, 1943:153).

A summary of data on clutch size is presented in Table 2. As far as possible, it includes only records of complete and incubated clutches. Even these records

TABLE 3

CLUTCH SIZE AND CHRONOLOGY OF NESTING*

Date	No. nests	Clutch Size Mean and S.D.**	Range
June 2–15	22	3.59 ± .67	2–5
June 16–30	28	4.89 ± .49	4–6
July 1–17	9	4.77 ± .25	4–5
	59	4.39 ± .43	2–6

*Based on 46 nests found during the present study and 13 nests located by Kent (**in litt.**) in 1951.
**Differences between means of early June and late June significant at the 99 per cent level; differences between means of late June and early July not significant.

could not be evaluated properly because laying rates were unknown or not stated in the paper. In at least two cases during this study, it was found that eggs damaged by predators were removed by the adults and incubation continued normally. Thus some small clutches reported in the literature may have been only part of a larger clutch. Four to five eggs are usual clutches in North America. Too few data are available to demonstrate latitudinal variation, but most clutches of six are reported from northern states. An even more interesting variation is suggested: of 46 complete clutches observed in this study, and 13 complete clutches found by Tom Kent in east-central Iowa (Kent, 1951, *in litt.*), all clutches found after mid-June—many of which may be renests or second nests—had four to six eggs; those found during early June had two to five eggs (Table 3). These differences are significant and demonstrate a pattern of seasonal change in clutch size which is the reverse of most double-brooded species (Lack, 1954:35), suggesting that the parents can feed more young in mid- than in early summer. A decline in clutch size in late summer is probable. This timing, as well as the late arrival and nesting of the species, probably is related to the chronology of available food organisms. Such a relationship has been shown for the Barn Owl (*Tyto alba*), which has a second and larger brood only when vole populations are high (Lack, 1954:35).

Also of interest for comparison is the clutch size of the Little Bittern (Table 4). While data are limited, it is apparent that clutch size of the European species is nearer six than five, as shown by both average and range. Clutches of eight have never been reported for the Least Bittern and clutches of seven are rare, but Witherby (1943:153) noted even larger clutches in the Little Bittern. He suggested that several females were laying in one nest.

Various workers have suggested that the Least Bittern rears two or three broods per season. No data from marked birds are available, but the chro-

TABLE 4

CLUTCH SIZE OF THE LITTLE BITTERN AS REPORTED IN THE LITERATURE

Area	Authority	No. nests	No. eggs in clutch
Germany	Groebbels (1935)	1	5
	Lucanus (1914)	1	7
Switzerland	Wackernagel (1950)	3	5
	Wackernagel (1950)	2	6
	Wackernagel (1950)	2	7
Holland	Wijnaendts (1954)	1	5
		10	5.8 Mean 5–7 Range
Less detailed; no. of nests not given:			
Germany	GroBkopf & Graszynski (1958)	–	7–8
	Steinfatt (1935)	–	5–6
Holland	Oort (1922)	–	5–7 (up to 8,9)
England	Witherby (1943: 153)	–	5–6 usual (also 4,7,8,9,10)

nology of nesting birds found during the present study suggests that two broods do occur (Fig. 2). These data undoubtedly are influenced by the varying intensity of nest hunting.

INCUBATION PERIOD

The incubation period of the Least Bittern has been determined as 15 days by Allen (1915), 16–17 days by Bent (1926), and 17 days by Bergtold (1917), but it was not clear from what point incubation was timed. Four nests observed in this study hatched in 19 to 20 days from the time of laying of the first egg (when incubation started) to the time when the first egg hatched. When timed by Heinroth's method (Nice, 1954) of counting from the laying of the last egg to the hatching of the last egg, incubation was 17–18 days in five nests. Using the same method, Baker (1940) reported a nest hatching in 18 days. Thus hatching requires only about three days while five to six days are required for laying the clutch.

Using Heinroth's method, data for the Least Bittern agree with that on Little Bitterns: GroBkopf and Graszynski (1948) reported 16.5 days, Oort (1922) found 17 days (range of 16–18 days), Groebbels (1935) reported 18–19 days, and Wackernagel (1950) approximately 19 days.

INCUBATION BEHAVIOR

Nest Maintenance and Incubation.—Incubation attentiveness is an extremely strong drive in bitterns. Chapman (1900), Allen (1915), Potter (1917), and Frost (1936) all reported birds which were so broody they could be

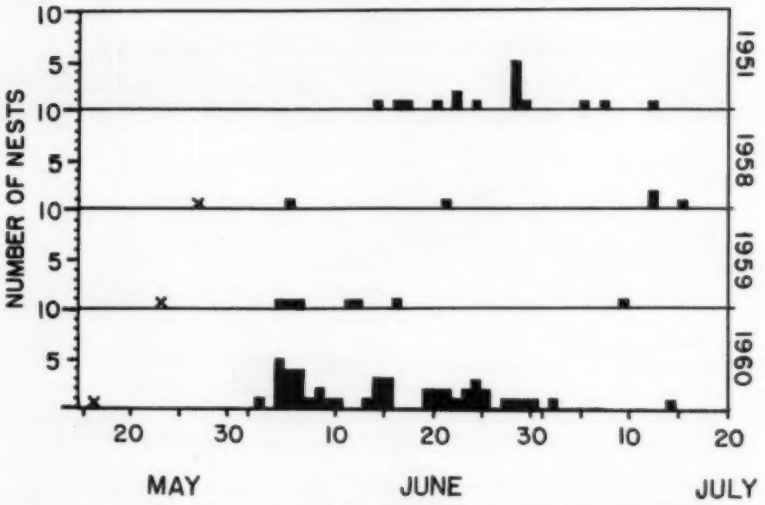

FIG. 2. Chronology of nest initiation in 1951 (Kent, *in litt.*) and 1958–1960 (present study). X = arrival of adults. Data calculated from either nest-initiation or hatching dates.

lifted from the nest. Two such birds were observed during this study. Wright (1946) found much individual variation among adult Least Bitterns which he studied, and Koenig (1953) reported similar variation among Little Bitterns and other European birds. During the incubation period, birds were never seen flying to the nest but landed in the nest area and approached the nest by quietly walking through the vegetation. Gabrielson (1914) reported that a clump of vegetation behind the nest was used as a landing site. The bird often hesitated at the edge of the nest to "roll" the eggs with the bill. Then it settled on the eggs by pushing the breast downward and rocking gently from side to side ("settling"). The posture maintained during incubation varies with the individual and the nest site. During long periods of incubation, the head is held low with the bill resting on the edge of the nest. The eyes are closed only occasionally.

Nest-building activities are few. Vegetation hanging over the nest is pulled down and worked into the nest. Continuous pulling of vegetation too strong to be pulled free results in a canopy. If the bird leaves the nest, it often returns with material which it adds to the structure. Or it may reach from the nest and pull material from the water. Experiments with artificial nests (see below) provided a source of material which was often utilized by the bird for its own nest.

TABLE 5

NEST BUILDING AND NEST JABBING IN RELATION TO STAGE OF THE NESTING CYCLE

	MALE		FEMALE	
	Minutes per poke or jab*	Observation time	Minutes per poke or jab*	Observation time
Incubation				
Nest 2 1958	—	None	30.0	6 hrs.
Nest 3 1958	12.0	6 hrs.	40.0	10 hrs.
Nest 1 1958	17.7	3 hrs., 50 min.	50.7	2 hrs., 32 min.
Nest 1 1959	20.9	5 hrs., 14 min.	29.5	3 hrs., 27 min.
Hatching				
Nest 1 1958	5.2	3 hrs., 48 min.	8.5	2 hrs., 50 min.
Nest 4 1958	10.9	2 hrs.	8.4	3 hrs., 30 min.

*This figure calculated from the number of "periods" of building activity, including "pulls," "pokes," or "jabs."

A nest-building action which appears more common than pulling of nest material—at least during the latter part of incubation—is "jabbing." With or without rolling the eggs with its lower mandible, the adult stares at the nest and jabs the bottom of the nest with either closed or open bill. This activity increases during the hatching period, but its exact function can only be hypothesized. Nest sanitation among the Ardeidae is commonly lacking (see Gross, 1923, on Black-crowned Night Heron, *Nycticorax nycticorax*; and Gabrielson, 1914, on the American Bittern), yet the Least Bittern uses a nest for nine days or more (Nero, 1950), and many nests remain exceptionally clean. Often a fragment of shell, a dragonfly wing or the feather sheaths of the young bird are the major evidences of nest use. Gabrielson (1914) noted one unsanitary bittern nest in river bulrush; a similar nest was found during the present study but was considered unusual. As with many young birds, defecation by juvenal Least Bitterns seems to be stimulated by the feeding of the parent and by handling. The fecal matter is of fluid mucous-like consistency. As the bird defecates, this fluid material flows over the nest material without clinging and flows through the holes in the nest. Possibly those holes formed by the "jabbing" activity of the parent assist in nest sanitation. Ryves (1946) considered sanitation as one of the possible functions of similar movements in passerines. Elimination of nest insects and aeration of the nest are other possible functions.

Table 5 summarizes nest-building activity such as pulling at vegetation, and jabbing the bill into the bottom of the nest. In three nests in which data were recorded during the incubation period, there were fewer periods of nest-building activity during incubation than during hatching. Also, it is apparent that the male performed nest-building movements more often than the female.

FIG. 3. Use of the wings in changing position on the nest.

Comfort Movements.—During long hours of incubation, turning is the most frequent movement. This is invariably accomplished with alternate opening and pushing with or refolding of the wings (Fig. 3). A quick rise and complete fluffing of feathers and shaking of the body is another common comfort movement. This may or may not be accompanied by preening, turning, poking, and settling. Partial shakes of either body or head also occur.

Gaping is common, especially following a period of alertness to food or intruders. A similar movement (Fig. 4) involves tongue stretching. Meyerriecks (*in litt.*) terms this "gagging" in the Green Heron (*Butorides virescens*). The

FIG. 4. Gagging.

FIG. 5. Preening.

bill is opened rapidly and more widely than in the threat posture. In one case, the gape was combined with a neck-stretch and wagging of the head and eventually the bird left the nest to drink, defecated, and returned to incubate. Another apparent fatigue-relaxing movement is the bill-stretch; the tips of the mandibles are held together but the mouth is opened proximally.

Irritations in the head region are scratched directly with one foot while balancing on the other. Body irritations are preened with a nibbling of the bill (Fig. 5). Extensive preening is usually started in the "ruff" of the lower neck—the powder-down area. Neck feathers are fluffed and individual feathers are preened with the bill tip from top to bottom. The mandibles are in slight but constant motion during the preening. The breast seems to be preened most often. Then the back of the lower neck, the belly, and flanks are preened but no definite order was noted. The greater primary coverts, primaries, and undercoverts are preened individually. There seems to be relatively little preening of the back. Feathers and other debris are removed from the bill by licking it with the tongue.

During warm periods, the head is held in any shady spot irrespective of the position of the body. Drinking is more common during warm periods and usually takes place a few feet from the nest. Panting is another means of cooling, and the "last resort" was seen in one case where the male left the nest, walked into water nearly three feet deep, and floated for a minute before returning to the nest and young.

After a rather long period of incubation, a female gave two calls not otherwise heard. The head feathers were fluffed, the head and bill were held vertically, and a *graa-wa-wa-wa* call given as the head and bill were returned

to their normal horizontal position. Later the same call was given but preceded by the *gack or quek*, which is a more common call given while on the nest.

Nest Relief Display.—Throughout incubation and brooding of the young, both sexes take turns on the nest. This change has a distinctive, though not elaborate, display. When one member of the pair comes to the nest, the incubating bird may ignore the oncomer, merely look alert, or assume a threat-like posture similar to that directed toward avian intruders. This seems to depend on the individual and the stage of the nesting cycle. The bird on the nest raises the crown feathers (these are also raised when drinking, leaving the nest, and with certain disturbances) and calls a low coarse *gra-a-a*. The oncoming bird, especially the male, has its crown and often its body feathers erect (Fig. 6a). When coming on the nest, both sexes shake their bills from side to side with the mandibles open, making a slight "rattling." At this time, the crown of the head is pointed toward the incubating bird and the bill points downward. This rattling seems very important in nest relief but also occurs when a lone bird of either sex returns to the nest after drinking. This posture was observed during incubation and brooding. Gabrielson (1914) described this action and noted a male doing this for fully 10 minutes before the female stepped from the nest and flew away. I have never observed a delay of this length, but one female refused to leave despite the fact that the male rattled for nearly five minutes. The male left and returned a short time later and repeated his performance. He finally entered the nest, whereupon the female departed. In this case, as in Gabrielson's study, there were young in the nest. At other times, the bird on the nest rarely hesitated. Usually, the bird on the nest also erects its crown feathers and stands. The oncoming bird depresses its crown feathers and assumes a posture with head lower than the standing bird (Fig. 6b). The air is one of cautiousness; at this time the necks may be crossed and the bill occasionally touches the back of the neck (Fig. 6b). The incubating bird then leaves (Fig. 6c), often taking flight from a nearby clump of vegetation.

On some occasions, the male of one pair placed a bulrush stem in the nest—but did not give it to the female as noted by Potter (1917). On another occasion, a female brought a stick of vegetation to the nest while the male was on the nest. Occasionally, sticks were brought back to the nest when birds of either sex left for food or drink. This type of behavior may be the forerunner of the more elaborate nest-relief behavior of other herons involving transfer of nest material.

Incubation by both sexes with a nest-relief display seems important to the strength of the nest attachment and to the maintenance of constant nest attentiveness. I never witnessed a bird leave a nest (under normal conditions)

FIG. 6a. (Top) Male approaching nest with crown and body feathers erected. Female has crown depressed.

FIG. 6b. (Bottom) Submissive attitude of female as she enters nest.

without first undergoing the nest-relief ceremony and having the mate take its place. When birds were flushed from the nest, the bird of the same sex always returned. Birds of either sex left to catch food, drink, or gather nest material but always returned within a minute and were not out of view of the nest. However, it appears that when both sexes are near the nest, the mate not on the nest will take over if one bird is frightened away.

Whether this display is truly vital to any change-over at the nest is uncertain. In an attempt to evaluate this, a stuffed male bird was placed on the nest. If the female returned, would she ignore a male which incubated rather than

FIG. 6c. Male's crest erected as female departs. Note her depressed crown feathers.

displayed? In two of the three trials on two different nests, males returned. Oncoming birds of both sexes approached cautiously, with typical erect crest and body feathers, and came on the nest despite the presence of the dummy. In all cases, they approached from behind the bird, hissed, and pecked it at the back of the head. To prevent desertion of the nest and damage to the skin, the incubating bird then was flushed from the nest.

Comparative Attentiveness of the Sexes.—The unique sexual dimorphism among the members of the genus *Ixobrychus* allows easy determination of relative attentiveness of the sexes in incubation. Groebbels (1935) presented data on one nest of *I. minutus*: in 14 hours and 35 minutes of observation, the female incubated the eggs 9 hours and 33 minutes while the male attended the nest only 5 hours and 2 minutes. Observations at five nests during this study totaled 54 hours and 39 minutes. During this time, the females incubated 32 hours and 35 minutes (59 per cent), while the males incubated only 22 hours and 4 minutes. Although there is a great deal of chance involved in which bird is on the nest when the observer is present, the length of the observations suggest that the female does most of the incubating. The longest period of incubation observed was by a female which incubated for five hours. During this time she left the nest briefly when frightened by the observer and then briefly when the observer left the blind. After an hour away from the nest, the investigator returned to find the female still incubating. Two additional hours of observation showed that the female incubated at least seven of the eight hours of observation. Several males incubated at least three hours, but longer observations were not available. Females did more feeding and drinking at the nest, presumably because they incubated for longer periods.

FIG. 7. Male watching food below nest.

Experiments with Artificial Eggs and Nests.—Experiments with artificial eggs and nests were attempted (1) to determine whether the sight of exposed eggs would stimulate incubation behavior despite the fact that the eggs were not in the proper nests, and (2) to learn whether both birds would incubate simultaneously if two nests were provided. In neither of two attempts did both birds appear. Nevertheless, birds of both sexes presented with artificial nests were much interested in them. One used the nest material for construction of its own nest. The rough-textured balsa eggs used in the first experiment apparently were not adequate to induce incubation but produced some interesting results. The balsa eggs were placed in the real nest and the real eggs were placed in the artificial nest. The male returned and immediately removed three of the balsa eggs and started over to the artificial nest. Then he returned to the real nest but obviously was not comfortable and finally left. The female came on immediately and without hesitation dropped out or carried away the two remaining artificial eggs; then she incubated on the empty nest, in full view of the artificial nest containing the real eggs. Apparently the nest is a stronger attraction than the displaced eggs when the nest is a conspicuous structure. Allen and Mangels (1940) reported similar behavior in Black-crowned Night Herons. Among species such as gulls which can easily roll their eggs into the nest, Tinbergen (1953) found that Herring Gulls usually preferred the eggs to the nest site but this depended on the local terrain.

Food Consumed.—During the intensive observation at nests, three females and two males were observed to feed while incubating. All birds spent considerable time observing the movements of prey items in the water below. When food is near, the crest and body feathers may be erected (Fig. 7) and

TABLE 6

FOOD ITEMS REPORTED IN THE LITERATURE

Authority	Number of birds	Foods
Adults		
Eifrig (1915)	1	2 sunfish
Gosse (1847)	–	small fish and crustacea
Roberts (1936)	2	crayfish (pincers removed) and snails
Saunders (1926)	–	small fish and arthropods
Simpson (1939)	7	small fish, insects, frogs, mammal
Wetmore (*in* Howell, 1932)	93	40% fish, 21% dragonflies, 12% insects, 10% crayfish, 18% miscellaneous
Young		
Gabrielson (1914)	–	frogs
Nero (1950)	–	minnows

gaping is common. Food which came within reach of the incubating birds made up most of the prey items, but the bird got off the nest and went to the water for prey for six of 34 observed feedings. Items taken were: five unidentified items, probably frog tadpoles; six unidentified insects; one grasshopper; 21 damselflies; and one tadpole. In addition, a male was observed feeding frog legs to the young. Despite the fact that snails were common around the nest, they were never eaten. However, Roberts (1936) reported snails in the stomachs of two specimens he examined. Success in capturing previously-spotted prey appeared to be nearly 100 per cent. There are relatively few data on food habits (summarized in Table 6).

Reaction of Adults to Potential Predators.—Chapman (1900) saw a Long-billed Marsh Wren (*Telmatodytes palustris*) pierce the eggs in a bittern nest; he regarded this as interspecific territory dispute. Common Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), and blackbirds may take eggs for food. Damage to only one egg in the nest does not always cause desertion; damaged eggs are removed and nesting continues normally. Marsh wrens, blackbirds, and Black Terns (*Chlidonias niger*) are often threatened by incubating birds by depressing the crown and withdrawing the neck preparatory to striking. Crown feathers may be raised and lowered when intruding birds are at a distance. When near, the bill is held open and a *gra-a-a* call may be given. The most intense aggressive posture involves withdrawing the head and spreading the wings with their dorsal surfaces facing forward. This posture is directed toward men (Chapman, 1900; Allen, 1915) and occasionally is assumed at wrens.

FIG. 8. (Left) Freezing behavior at the approach of a Great Blue Heron.
FIG. 9. (Right) Female removing egg shell from the nest.

Two observations were made during the present study which suggest behavior toward large predators. In one, a female suddenly rose from the normal incubation posture to the "freeze" (Fig. 8), and a Great Blue Heron (*Ardea herodias*) flapped over. The same female and another were observed watching buteos which were soaring at such heights that they could not be identified by the observer. That buteos may prey on bitterns was assumed when a young Red-tailed Hawk (*Buteo jamaicensis*) was found standing in water on a weak but live adult female bittern.

Predators on young probably include turtles, as Trautman (1940) saw one take an adult. During this study, several dead and partly eaten young bitterns were found in the water near a nest. The absence of fish in the lake implied that turtles were responsible. A garter snake (*Thamnophis ordinatus*) was observed which was attracted to young bitterns, but Kent (1951) saw a water snake (*Natrix sipedon*) pass directly over a nest without attacking the young.

HATCHING SUCCESS

Of 38 nests observed for hatching data, at least one egg hatched in 32 (84 per cent). Average clutch size of this group was 4.0, and averages of 3.5 young were reared per successful nest and 3.0 for all nests observed. These

success data are believed to be biased upward by the fact that most nest loss occurs during the first few days of laying and building when eggs are more likely to be exposed. Few nests were found in this early stage but many empty nests were located which probably had been deserted. Because these nests could not properly be evaluated, only nests with complete histories were used for success data.

CARE OF THE YOUNG

Behavior of Adults During Hatching and Rearing.—During hatching and rearing, the adults seem more hesitant to leave the nest. Nest relief displays by the oncoming bird are more intense and of longer duration. When the brooding bird finally leaves, it may stay away for only a short time. Hatching is often observed closely by the adult and as soon as the young are free from the shells, these are carried away (Fig 9) and dropped in the water or eaten.

After the young are free of the shell and before they are dry, they are fed by regurgitation. Apparently, the adult's bill must be lowered to the young before feeding occurs. If hungry, the young grab the bill violently (see Bates, 1943, for a description of this in the Little Bittern). However, the bill may be raised again if the adult is not ready to feed. The stimulus causing feeding response in adults is not clear. The adults seem to feed only if the young are active. The young open the bill in a fashion similar to the gaping of passerines but this does not seem regular. "Peeping" calls by the young seem more prevalent when they are hungry and may serve as the releaser. Or, the bill of the young may be a stimulus when it is held vertically (as when hungry) but not when held horizontally or slanted so that the down of the head hides the bill from view.

Gabrielson (1914) noted that all young in a nest were fed at each feeding, but Davidson's (1944) data indicated that this varied. In general, feeding of young occurs only when the young grab the bill—again suggesting that food is only regurgitated by a sign stimulus from the young—and therefore the number of young fed depends on their desire to feed. Gabrielson found that the young were fed only four times in one day, and Davidson's (1944) data also suggested a limited feeding schedule. During the present study, only two of the five nests were observed for a significant period after hatching. During 11 hours and 54 minutes of observation on two of these nests, females were on the nests 6 hours and 6 minutes and males brooded 5 hours and 48 minutes. During this time, females attempted to feed some or all young once every 20 minutes while males fed every 10 minutes. This agrees with statements by Gabrielson (1914) and by Breckenridge (*in* Roberts, 1936:194) that the male does most of the feeding. However, the rate of feeding undoubtedly varies with the age of the young and the nature of the food.

Young may be shaded by an adult standing over them (Fig. 10).

FIG. 10. Shading of young and panting and sunning by the male.

Innate Responses of the Young.—When just free from the shell and still wet, the young bittern is equipped with those reflexes vital to its survival. The gripping response of the feet is weak but apparent whenever the bird is moved or its feet are removed from a solid surface. If turned on its back or side, it attempts to right itself by swinging its feet and grasping. When held on an inclined plane, the feet push forward and prevent the bird from slipping. The bird is nearly able to hold itself on a branch when newly hatched and birds one day old or more certainly can keep from falling from the nest by this means. At several days of age, the bird can firmly grip twigs and remain in that posture for some time (see Nero, 1950). When gripping a piece of vegetation, the bird uses its wings and curved neck as well as its feet and counterbalances the body with the head.

The eyes are closed for nearly ten minutes after the bird leaves the shell and it does not respond to artificial bills for about 35 minutes. At that time, it can hold its head up for only a few seconds. Two moves are apparent within 15–20 minutes after hatching; the bill is opened in a quick gape-like movement but is not held open as in passerines. Also, the base of the bill is stretched as in adults. The ability to hold up the head possibly is vital to survival for the adult is probably stimulated to feed by the raised head of a hungry bird. The juvenile is attracted as soon as the adult's bill is placed before it. It feebly moves the bill toward the adult's bill and turns its head

in order to grip the adult's bill. The regurgitated food then passes down the adult's bill and commonly strikes that of the juvenile. As the juvenile's mandibles follow the food down to the tip of the adult's bill, the food is easily taken. In this fashion, the young also are directed to food which may fall into the nest and the young quickly learn to recover this. During early feedings, the adults recover any food dropped into the nest. On one occasion, two young of three or four days of age were competing for a pair of hind legs of a frog. This invariably resulted in each getting one of the two legs and a tug-of-war ensued so that the legs fell to the bottom of the nest. The small size of the young and the large size of the legs prevented recovery by the juveniles. The male reswallowed and regurgitated this pair of legs eight times and the result was always the same! The legs were still not consumed when I was forced to leave the blind.

As the young reach about three days of age, they respond to any nonbittern form by "freezing." At five to seven days, they assume the aggressive posture with the neck down, the head ready to strike, and the wings held open with their dorsal surfaces facing forward. Portielje (*in* Tinbergen, 1953:214) showed that a distinct head shape was essential in models to release the striking attack of European Bitterns. During this posture, young Least Bitterns sway back and forth from side to side. This behavior is common in adult American and Least Bitterns and reportedly occurs as a camouflaging mechanism when marsh vegetation is moved in the wind (Saunders, 1926). However, Elliott (1951) reported this behavior in a captive Least Bittern indoors. At six to nine days, the young leave the nest, apparently to seek shade and possibly to feed as well. They move through the reeds with great skill but occasionally get wet in doing so. Their color is light tan, common to the young of many marsh birds, and they are well camouflaged in the nest and in old vegetation. They return to the nest when the adult comes to feed them. Whether or not the adults feed the young in the vegetation is not known. Nero (1950) had to fence birds to keep them at the nest but also found banded young in the area of the nest at 27 days of age (Nero, 1951).

Experimental Analysis of Feeding Responses of Juveniles.—That the adult's bill is the stimulus for feeding behavior in juveniles and that there is a simple innate response in juveniles is indicated from tests with model bills. A yellow pencil was sufficient stimulus for some birds, and one juvenile of six to seven days of age grabbed the yellow leg of the male and tried to feed! Unfortunately, too few young were available to test all newly hatched young without the influence of learning and to make tests statistically significant. Nevertheless, they indicate an instinctive feeding response.

Models of flat cardboard and three-dimensional models of cardboard and wood were used. There was no difference apparent, but three-dimensional

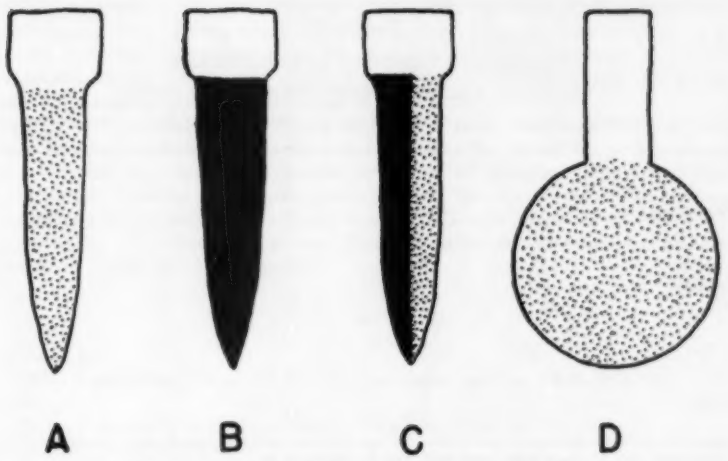

FIG. 11. Models used to test feeding responses of young.
A = yellow or gray; B = black; C = black and yellow; D = yellow or gray.

models of wood were selected for use in the field because of their durability. These were painted gray, black, yellow, and yellow and black (Fig. 11). In testing, the bill was held vertically in front of a bird and moved up and down gently for five seconds. The response was recorded as positive or negative, although several grabs at the bill often were made during that period. Most tests were performed on birds of one to four days of age although aggressiveness at the latter age occasionally voided results. Some birds were sleepy and could not be awakened; others were not stimulated by the bill and probably had just been fed by the parents. Those tests which produced some positive results are summarized in Table 7 and show that any elongate object may produce a grabbing response. The effectiveness of gray was surprising and stresses the value of an elongate form as part of the releasing mechanism. To test the significance of color, gray cardboard was cut in a circular form (Fig. 11) and painted yellow on one side. In tests, the yellow stimulated a feeble pecking (not grabbing as with bill models) but gray resulted in no response. Thus, color as well as form is part of the releaser which causes feeding behavior. When birds were presented the cardboard circles, it is of interest that very little effort was made to turn the head, and pecking was directed at the edge. Similar tests with a square model provided similar results but with greater tendency to turn the head parallel to the edge of the model. The importance of parallel positioning of juvenile and adult bills as a second step in releasing feeding response was tested by presenting artificial

TABLE 7

RESPONSE OF YOUNG BIRDS TO ARTIFICIAL BILLS

(NUMBER OF POSITIVE RESPONSES OVER NUMBER OF TESTS)

Age of young	Gray	Black	Yellow	Black and Yellow	No. of Individuals
Newly hatched*	0/6	0/6	6/6	4/5	6
1-4 days	11/16	10/31	25/31	28/30	16
Totals	11/22	10/37	31/37	32/35	22

*At least two of these had never been fed by the parents.

bills to young in a horizontal position. A positive response resulted in 8 of 13 trials.

Based on present limited data, the response of young birds seems to be a two-step reaction. The elongate form and yellow color stimulate an initial reaction. Secondly, the juvenile presumably aligns its normal line of vision so that the adult's bill is horizontal. Both sexes have a reddish base to the bill and this is brighter in the male than in the female (and the male does most of the feeding), but the significance of this red area as a releaser was not tested experimentally.

SUMMARY

The nesting behavior and habitat of Least Bitterns was studied in several glacial lakes and marshes in Iowa. Eighty-nine nests were found, and intensive observations from blinds were made at five nests. Nests were mainly in *Typha* spp., *Scirpus acutus*, and *Scirpus fluviatilis*. Clutch size varied from two to six eggs with the smaller clutches being found early in the season. Copulation occurs on the nest during early incubation and possibly there prior to incubation. Incubation required about 19 days from the laying of the first egg to hatching of the first egg and 16–17 days from the laying of the last egg to the hatching of that egg. The species appears to be double-brooded in Iowa, at least in some years.

Nest incubation movements are: bringing material to the nest, pulling in material from above, and bill-jabbing in the nest bottom. During incubation, the bird rolls the eggs with the lower mandible, settles on the eggs by a rocking motion, and remains alert during even long periods of incubation. Comfort movements were shaking, turning, gaping, scratching, preening, drinking, and panting. Both sexes incubate, and nest relief includes a simple display of erecting the crown and body feathers, "rattling" of the bill, and

occasional crossing of bills or touching of bill to back. The oncoming bird slips under the incubating bird. During nearly 55 hours of observation, the female incubated 59 per cent of the time. Incubating adults fed on passing damselflies and other insects, and occasionally left the nest to take nearby prey. Wrens, blackbirds, hawks, snakes, and turtles are thought to prey on eggs, young, or adult bitterns.

During hatching, adults remove the egg shells or eat them. Both sexes feed the young by regurgitation but the male feeds more often than does the female. Innate responses of the young which are considered important to survival are gripping of the feet, holding vegetation with the wings, and balancing with the head. The stimulus for feeding in young probably is a yellow-colored and elongate structure. These releasers were tested briefly experimentally. The releaser for parental feeding behavior is unknown but is probably the sight of raised bill of the juvenile.

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LATE-SUMMER FOOD OF RED-WINGED BLACKBIRDS IN A FRESH TIDAL-RIVER MARSH

BROOKE MEANLEY

IN late summer, during molt, large numbers of Red-winged Blackbirds (*Agelaius phoeniceus*) feed and roost in marshland, and from there make forays into the uplands. Certain fresh tidal-river marshes in the Delaware Valley and Chesapeake Bay region where there are great beds of wild rice (*Zizania aquatica*) attract hundreds of thousands of redwings.

The period when wild rice seed is available coincides with the ripening period of a part of the corn (*Zea Mays*) crop. The availability of rice has been shown to reduce feeding pressure on corn. Robert T. Mitchell (1953. U.S. Fish and Wildlife Service unpublished report) found that in the lower Delaware River Valley damage was heavier in fields where corn matured before and after the wild rice than in those where corn ripened during the time the wild rice seed was available. The following year Mitchell and John T. Linehan reported (1954. U.S. Fish and Wildlife Service unpublished report) that damage to cornfields adjacent to marshland was three times as great as to comparable fields farther from marshland.

The importance of wild rice and other marsh plants to the redwing during the period when wild rice seed is available, was studied further in 1958 and 1959. Results are reported in the present paper. Field observations were made in wild rice beds in a 200-acre fresh tidal marsh on the Patuxent River near the mouth of Lyon's Creek, Anne Arundel County, Maryland (Fig. 1). Additional food-habits data were obtained by analysis of stomach contents of 130 birds collected while they were feeding in the marsh. Collections were made between 8:00 AM and 4:00 PM, from 5 August to 30 September. Birds that left the area before 8:00 AM or arrived after 5:00 PM were not collected because it was not possible to be sure that these birds were using the marsh as a feeding area.

THE PLANT COMMUNITY

The Patuxent River marsh is typical of the fresh tidal-river marshes of the coastal plain province. Similar marshes are located in the upper reaches of most coastal-plain rivers. They are characterized by the richest mixture of marsh flora of any of the major marsh communities in the Chesapeake Bay area.

Important plants in this community are wild rice, three species of smartweed (*Polygonum*), Walter's millet (*Echinochloa Walteri*), river bulrush (*Scirpus fluviatilis*), spatter-dock (*Nuphar luteum*), arrow-arum (*Peltandra virginica*), arrowhead (*Sagittaria latifolia*), pickerelweed (*Pontederia cordata*), marsh-

FIG. 1. Fresh tidal-river marsh, Patuxent River, Maryland. The dominant vegetation here is wild rice.

mallow (*Hibiscus* sp.), rice-cutgrass (*Leersia oryzoides*), water-hemp (*Amaranthus cannabinus*), and two species of cat-tail (*Typha latifolia* and *T. glauca*).

Seed production is at its peak during August and September. Rice seed is produced from about 15 August to 15 September; dotted smartweed (*Polygonum punctatum*) from mid-July to 30 October; and millet from about 15 August to 15 October. The seeds of halberd-leaved tearthumb and arrow-leaved tearthumb (*Polygonum arifolium* and *P. sagittatum*) are present in quantity after 1 September; and rice-cutgrass after 15 September.

FIELD OBSERVATIONS

Hordes of redwings begin to invade the Patuxent River marsh soon after the nesting season. This is in late July and about the time of the onset of molt. Wild rice towers over all other marsh plants and blackbirds frequently use it for perching. The wild rice is then in bloom and the birds occasionally eat the staminate flowers. This may be done while the birds search for seed which has not yet formed, for the flowers do not seem to constitute an important part of the diet. The marsh during this period may contain hundreds of redwings hovering in the air as they grasp the panicle or seed head of the rice plant in an attempt to loosen flower or developing seed.

The ripened rice seed is long, slender, cylindrical, and armed with an even longer and more slender awn and a thin hull covered with short stiff bristles. A feeding bird removes the hull by holding the seed crosswise and revolving it in its bill. Birds feeding on wild rice often acquire a greenish stain on the sides of their bills near the base.

As the wild rice and dotted smartweed reach optimum seed production the redwing nears the height of its molt and begins to restrict its activity. The population in the Patuxent marsh probably is at its maximum at this time. An estimated 50,000 birds were roosting there on 2 September 1959.

Although the marsh offers both a retreat and source of food, at least some of the birds do part of their feeding elsewhere. Throughout the period of wild rice availability, corn continues to show up in some gizzards. Also, some molting redwings, without tail and minus some flight feathers, were seen in labored flight to upland areas.

By the end of September, any remaining wild rice seed is embedded in the mud. By this time most birds have completed their molts. Some have begun to migrate and the great summer flocks have diminished in size.

Adults fed more commonly on wild rice in the Patuxent marsh than did juveniles. Of 130 redwings collected at random while they fed on rice, only 11 were juveniles or birds of the year. The same preponderance of adults was found among birds caught by mist-netting. There were only 40 juveniles among 300 redwings netted in daylight hours from 15 August to 15 September.

STOMACH ANALYSIS

Seeds of marsh plants formed the bulk of the food of redwings collected, (Table 1). Dotted smartweed, wild rice, and Walter's millet were the most important. Dotted smartweed occurred in 93 stomachs and comprised 38 per cent of the total volume of food in the series of 130 stomachs examined. Seeds of smartweed may have been utilized to a greater extent than seeds of other marsh plants because they were easily obtained and were available in greater quantities and over a much longer period than any other marsh seeds. Even during the optimum period of wild rice availability, the smartweed was utilized 15 per cent more than rice.

Other smartweeds, the large-seeded halberd-leaved tearthumb, and the arrow-leaved tearthumb, generally mature after 1 September. They are not so abundant as dotted smartweed and were relatively unimportant in the redwing's diet during the period covered by this study. Rice-cutgrass and water-hemp also were relatively scarce and fall in this category.

Walter's millet occurred in 62 stomachs and formed 11 per cent of the total volume. Large flocks of female redwings were constantly observed feeding in beds of this millet, whereas males rarely were seen there. Seeds of

TABLE 1

FOOD OF 130 RED-WINGED BLACKBIRDS COLLECTED DURING LATE SUMMER IN THE PATUXENT RIVER MARSH

Food	Per cent of stomachs	Per cent of total volume
PLANTS		
Dotted smartweed	88	38
Wild rice	61	24
Walter's millet	46	11
Corn	26	12
Halberd-leaved tearthumb	18	4
Ragweed	4	1
Panic-grass (*Panicum* sp.)	3	1
Arrow-leaved tearthumb	3	1
Rice-cutgrass	3	1
Crab-grass	2	Trace
Wheat	1	1
Undetermined native grasses	1	Trace
Water-hemp	Trace	1
INVERTEBRATES		
Beetles, mostly weevils	48	1
Grasshoppers	12	3
Undetermined insects	12	Trace
Caterpillars	3	1
Leaf-hoppers	3	Trace
Spiders	3	Trace
Stink-bugs	2	Trace
Ants	1	Trace
Giant water-bugs	Trace	Trace

this plant occurred in stomachs of 51 of the 67 females, but in only 11 of the 63 males.

Corn appeared in 35, approximately one-fourth, of the stomachs. The presence of this grain in stomachs from birds collected while they were feeding in the marsh supports the field observation that redwings visit the uplands even when smartweeds, wild rice and millets are abundant in the marsh. Further evidence of forays into the uplands is the presence of minor quantities of the following seeds in the stomachs: ragweed (*Ambrosia artemisiifolia*), crab-grass (*Digitaria* sp.), other undetermined native grasses (Gramineae) and wheat (*Triticum aestivum*).

Insects, of which Coleoptera and Orthoptera were the most important, formed only 5 per cent of the total volume of food consumed. Weevils (Curculionidae) occurred in 44 stomachs, and were taken more frequently than other insects, possibly because these slow-moving insects were easily caught.

Other insects taken included caterpillars (Lepidoptera), leaf-hoppers (Homoptera), ants (Hymenoptera) and stink-bugs (Hemiptera). Spiders (Arachnida) occurred in four stomachs. Only one aquatic insect, a giant water-bug (*Belostoma* sp.), was taken.

DISCUSSION

Red-winged Blackbirds spend a great amount of time feeding on marsh foods during late summer, and their depredations on corn fields apparently are reduced. However, the great attraction of wild rice and smartweed results in an influx of vast numbers of redwings to fresh tidal-river marshes, thus creating great potential pressure on adjacent corn fields. The presence of corn in stomachs collected in the marsh, and the obvious devastations in corn fields adjacent to marshes, indicate that the protection to corn is incomplete and that its importance should not be overemphasized.

SUMMARY

During late summer in the Delaware Valley and Chesapeake Bay region, hundreds of thousands of Red-winged Blackbirds feed in wild rice beds of fresh tidal-river marshes. The period during which wild rice seed is available coincides with the ripening period of a part of the corn crop, and there is evidence to indicate that the availability of the wild rice reduces bird feeding pressure on corn in the area. The importance of wild rice and other marsh plants to the redwing during the period when wild rice seed is available was studied further by field observations and by analysis of stomach contents of 130 birds collected in wild rice beds of the Patuxent River in southern Maryland. Seeds of marsh plants formed the bulk of the food of redwings collected. Dotted smartweed, wild rice, and Walter's millet were the most important food plants. Corn was the fourth most important item. It occurred in 35, approximately one-fourth, of the stomachs.

PATUXENT WILDLIFE RESEARCH CENTER, LAUREL, MARYLAND, 2 MARCH 1960

WEATHER AND EARLY SPRING MIGRATION IN IOWA

BETH PROESCHOLDT

IT is generally accepted that certain weather conditions are associated with migration, as shown in studies by Bagg *et al.* (1950), Williams (1950), Gunn and Crocker (1951), and many others, although there is considerable speculation as to whether the reaction is to the general weather situation as such, or to one or more particular factors linked with it (Lack, 1960; and others). In this study I have attempted to analyze the meteorological events that were associated with a migration of 18–24 March 1959, at points in Iowa, as well as in a reverse migration on 25 March in north Marshall County, Iowa.

To supplement my information I wrote to several observers whose kindness in sharing their records was much appreciated. Valuable assistance was given by Henry Hurst, meteorologist of the U.S. Weather Bureau, Des Moines, Iowa, in supplying and interpreting certain weather data. To Dennis Carter I am grateful for reading the manuscript and offering suggestions.

NORTHWARD MOVEMENT

The mid-March weather in Iowa was dominated by a high-pressure system that by 18 March was centered over West Virginia. This followed a huge low-pressure cell that had moved northeastward—the "low" that on 14 March had brought Iowa its second blizzard in ten days. Temperatures soared on 18 March as the clockwise wind circulation around the high-pressure center gave Iowa southerly winds and bright sunshine, weather typical of the westward portion of a high-pressure area. These conditions accounted for the first period of continuous 24 hours of above-freezing weather of the season. A low-pressure area, while not originating in the southwest as in the ideal situation described by Bagg and his colleagues (1950), but centered over central Manitoba, intensified the southerly winds. This weather was favorable to a strong northward movement of birds into Iowa, pressure-pattern flying as described by Bagg *et al.* (1950), involving following winds and rising temperatures. Williams (1950) found that high temperatures were associated with big rushes in spring; Devlin (1954) associated spring migration with southerly winds; and Dennis (1954) found that warm weather and southerly winds were favorable to northward departures from Texas.

At Spirit Lake on 18 March, James G. Sieh noted the first influx of waterfowl and blackbirds. This movement continued for several days.

Although a cold front with strong NE winds crossed the state on 19 March, migration continued, with Dr. Milton W. Weller noting the first big push in northern Story and southern Hamilton counties. Blackbirds, Marsh Hawks

(*Circus cyaneus*), Common Crows (*Corvus brachyrhynchos*), Mallards (*Anas platyrhynchos*), Pintails (*Anas acuta*), and Snow Geese (*Chen hyperborea*) were well disturbed. "All were battling strong northeast wind," observed Dr. Weller.

Iowa was on the eastern edge of a high-pressure center on 20 March, with light northerly winds and slightly cooler temperatures. That day Fred Kent observed near Iowa City "a huge influx of new migrants," Common Grackles (*Quiscalus quiscula*), Robins (*Turdus migratorius*), Red-winged Blackbirds (*Agelaius phoeniceus*), ducks, gulls, hawks, shrikes, meadowlarks, and others. These birds, perched in trees and flying, were apparently mostly overnight arrivals.

On 21 March northerly winds sent temperatures 15 to 20 degrees below normal. However, Fred Kent counted additional arrivals, ducks and hawks, in his area.

The days of 19 March through 21 March had weather characteristic of the eastern side of a "high" (generally thought to be more unfavorable to migration), and included accompanying northerly winds considered adverse winds by Imhof (1953:188): "Birds are generally grounded by strong head winds, but when the winds lessen they probably move on." The birds observed had possibly been held back by the snows and cold weather of the first two weeks of March—the relationship postulated by Hinde (1951:336) and cited by Lack (1960): "if the internal changes are well advanced then migration may occur even under apparently unfavorable conditions. . . ."

By 22 March, Iowa was again on the western edge of a high-pressure area, with strong southerly winds and fair skies. On that morning in north Marshall County, I saw many mixed flocks of blackbirds flying north, only a prelude to the movement observed later. In the afternoon migration continued at an accelerated rate. From 3:00 to 4:00 PM I saw approximately 25,000 blackbirds of various species pass over the fields. In one five-minute period in that hour I estimated at least 7,000 birds passed. As each flock of 80 or 100 birds passed I lifted my binoculars for a better look, and behind them, out of eye-range but clearly visible with binoculars, 300 to 500 birds were visible flying northward. For many minutes, as this pattern of heavy movement continued, there was not a moment when a large group of birds was not passing or pausing to rest in fields or trees close by. Some of these flocks were of blackbirds of different species, some were entirely of Common Grackles, some were entirely of Starlings (*Sturnus vulgaris*), with smaller numbers of Red-winged Blackbirds. Thousands of birds must have passed this one pinpoint on the map during the day, for migration continued for the remainder of the afternoon. A more detailed study of the 22 March weather reveals that a low-pressure area, while again not originating in the southwest,

but centered that day over the Saskatchewan-Manitoba border, intensified the southerly winds in this area. This situation (similar to that of 18 March) is described by Hochbaum (1955:118) as a "trough of southerly winds moving up the middle of the continent." In our area the warm front associated with the low-pressure system arrived at 12:00 PM on 22 March, and the cold front reached here around 1:00 PM, 24 March. So for 49 hours we were in the warm sector of the "low," the time of the strongest observed movement of birds. Bagg *et al.* (1950), Lowery (1951), and others found that in spring pronounced movement occurs during this interval. During the hour of greatest observed activity, from 3:00 to 4:00 PM on 22 March, the wind was south at 21 mph with gusts to 33 mph, with clear skies and temperatures from 52 to 55°F.

With our area still in the warm sector of the low on 23 March, the temperatures climbed into the 70's in southern and central Iowa with SW winds averaging 13 mph, and fair skies. The lowest barometric reading of the period, 29.80 inches, was reached at 4:00 PM and remained within .02 inches of that reading until 6:00 AM, 24 March. Robbins' study (1949) showed that "seven of the nine flights occurred at minimum points in the pressure curve, and the other two took place only one day away from a minimum." This minimum barometric reading, therefore, was only one day away from the strong movement of birds on 22 March, and coincided with Fred Kent's observations near Iowa City of "more ducks, Red-tailed Hawks, and huge flocks of blackbirds" on 23 March. Migration in north Marshall County continued in full swing on 23 March and the morning of 24 March, with gulls, Snow Geese, Killdeer (*Charadrius vociferus*), and hundreds of blackbirds on the move.

At about 1:00 PM on 24 March, the wind veered to the north as a slow-moving cold front (marked stationary on the weather maps) crossed the state. However, the warm air moving around the low had moved a great amount of warm air to the north of the quasi-stationary front, and the front had to move southward considerably before the cold air reached Iowa.

REVERSE MIGRATION

On 25 March the sky was heavily overcast with a NE wind ranging from 12 to 23 mph, and gusts to 34 mph, weather associated with high pressure. The center of this high was around Hudson Bay, with the clockwise winds bringing cold arctic air into Iowa. That morning in the village of Liscomb, in Marshall County, about 100 Slate-colored Juncos (*Junco hyemalis*) flew into our trees and bushes and gradually worked in a northerly direction. They were the only birds observed going north that day. All other birds seen were exhibiting what seemed to be a reverse migration. During the morning hours several

small blackbird flocks and one group of 30 Robins were seen flying south over our house. At 1:15 PM about 300 blackbirds of various species arrived from the north, paused to rest for a few moments in our trees, then flew off to the southwest. At 4:00 PM approximately 1,000 blackbirds were seen approaching from the north and heading south parallel to the Iowa River bottomlands. This flock was moving in a slowly-swirling manner. By this time a light rain was falling as a low-pressure (storm) area moved northeastward from the Oklahoma-Texas region.

During the night, with the temperature hovering just above freezing, rain accompanied a strong gusty NE wind. All the next day, 26 March, in Marshall County, rain fell intermittently, mixed at times with sleet and hail. Rain fell across the state, with up to two inches in central and southern Iowa and up to five inches of snow in northern Iowa. Hail and high winds accompanied the rain in some areas. Early on 27 March the low-pressure cell responsible for the storm moved out of the state and completed that weather cycle.

DISCUSSION

There seems to be no doubt that the birds observed moving south or southwest on 25 March were reversing their normal migration pattern for that season. It would seem that these birds were retreating before the much colder air and strong northerly winds associated with the eastern edge of a high-pressure area. Just as clearly, the migration movement earlier discussed was associated with another combination of weather. This mass northward movement would seem to have been initiated on 18 March, with weather typical of the western edge of a high-pressure system—strong southerly winds and fair skies, with an opposing low-pressure area intensifying the winds. Another similar weather pattern on 22 March, along with the warm sector of the low-pressure system, was favorable to continued migration of "wave" proportions until the adverse weather following the cold front of 24 March arrived.

SUMMARY

This study outlines the weather in March 1959 that was favorable to a strong northward movement of birds observed in Iowa. Meteorological conditions also appeared to effect a reverse migration. The weather associated with the northward movement was that of the western edge of an area of high pressure and the warm sector of a low-pressure system. The reverse migration followed weather associated with the eastern edge of a high-pressure area with a cold front and northerly winds, and occurred just before a severe storm from the southwest entered the area.

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LISCOMB, IOWA, 15 FEBRUARY 1960

SOME SIZE GRADIENTS IN NORTH AMERICAN BIRDS

A. L. Rand

In 1871, J. A. Allen wrote that increase in size with increase in latitude was so well known for the birds of eastern North America that any further demonstration of it was unnecessary. Hamilton, in 1958, writes that he can find little evidence for the application of Bergmann's rule (wing length and presumably body size being greater in colder climates) within New World species. Obviously these two statements need to be harmonized!

HISTORICAL NOTE

There has been a great deal of work done on correlating patterns of geographical variation in size of birds since J. A. Allen wrote. The situation has been found to be much more complex than a simple increase in size with a decrease in temperature.

Allen was writing in the infancy of the study of geographical variation. He was attempting to codify it by the use of a subspecies concept, and also to codify it by formulating rules outside the use of the subspecies concept. This was the pioneer stage.

A second stage was reached in regard to subspecies when the concept was accepted and an attempt was made to indicate all geographical variation by subspecies names. A third stage is being reached with the realization that every even moderately separated population probably differs from every other, and that to name as a subspecies every one that can be shown to be different in some way would stultify the concept and render it completely useless. Subspecies names as used by many taxonomists now indicate only some of the more obvious geographical variants.

Indeed some students of geographical variation are groping for a more useful way to indicate geographical variation than using taxonomic nomenclature. A system of numbers or letters, in effect a formula, has been suggested, and has actually been used in analyzing variation in some species. But until human mentality will use latitude 40° 42′ N; longitude 74° W for Manhattan Island, instead of saying New York City, subspecies names will not be entirely superseded by formulae.

Concepts of zoogeographical rules, which deal with the same material in part as do subspecies, are in somewhat the same situation as subspecies concepts. They have passed through the same phases: (a) being established, (b) attempts made to cram all observed variation into them, (c) the realization that environmental factors are so complex and interacting that our "rules" can hope to outline only parts of the more obvious correlations. The dissatisfaction with "rules" is part of the same dissatisfaction with subspecies, and

the solutions of both are bound up together. The fact that "rules" for the character gradients are less sharply defined, especially in the allocation of single specimens, has delayed their re-evaluation. The most important step has been the generalization of Huxley in pointing out that a more general, neutral term, cline, can be used for any character gradient without attaching an interpretation to it. Certain apparent exceptions are characterized as stepped clines, and it is realized that while one cline in one character may have a certain geographical pattern, another character may show a different pattern.

CLIMATE AND GEOGRAPHY

That northern localities have colder temperatures than more southern ones is only partly true. It is true in general for the United States east of the Rocky Mountains, with average annual temperatures in southern Florida of 75° F., and Texas of 70° F., and in northern Maine of 40° F. and central North Dakota of 40° F., and a rather regular decrease from south to north in between (excepting the small area of the Alleghanies). However, while the isothermal lines in this area run more or less east and west, the case is different in the Rockies and west to the Pacific Coast. Here many of the isothermal lines have a north-south trend, and areas in both Montana on the Canadian border, and in northern New Mexico (600 miles farther from the north pole than Maine) have 40° F. as the average annual temperature.

That is, in the eastern United States (except for the Alleghanies), latitude is a good guide to temperature; in the west it is a very poor one. (U.S. Dept. of Agri., 1941, p. 703, with different facets of the climate mapped on following pages.)

Rainfall gives a somewhat similar picture, with rainfall decreasing from 60 inches on the Gulf of Mexico to 30–40 inches in the northeast United States; much of western North America and northeastern Canada have less than 20 inches. However, the picture near the Pacific Coast is complicated.

SIZE

The word size continually appears in discussing some character gradients. In the present state of the study of geographical variation in birds, the use of the word size has not the necessary precision. In more popular writing it has its place, where it may mean wing length, total length, weight, or apparent bulk. But in more technical papers it should be replaced by the measurement which is actually meant. Allen equated wing length with weight, and this assumption is still common. While it is valid in some cases, it is not always true. If accepted for samples of birds of the same species from distant areas with widely different environments, there is danger of falling into grievous error.

The available data on weights are poor, incomplete, and scattered. One is tempted to apologize when using them. But there are some data available, and it is better to use them than to depend entirely on speculation for data when discussing weight variation and its implications.

SIZE AND GEOGRAPHY

The wing length of a species may remain fairly uniform over a wide area, as is well shown by the Ruffed Grouse (*Bonasa umbellus*), which ranges from northern Georgia to Nova Scotia and west to Alaska and northern California. The species breaks up into 12 races, based mainly on color, yet the average wing length of subspecies varies only from 178 (once) and 181 to 186 mm. (Aldrich and Friedmann, 1943).

However, variation in wing length is sometimes considerable, and we look for parallel variation in different species and hope to find this correlated with environmental factors. Even if such correlations are real, we can hardly expect the same set of factors to be operative over the whole of North America, with its wide range of environments. They vary from subtropical in southern Florida, forests and prairies of the lowlands and hills of the eastern and central part of the country, arctic barrens of the north, and the deserts, scrubs and forests of the mountains and valleys of the western part of the continent. Consequently I have presented the data by geographical areas within which some consistency is evident or to be expected. While I have confined myself largely to cases where both wing length and weight are available, I have also kept in mind that there is a greater body of data on wing length alone, which may be indicative and at least points the way to further investigation.

Ideally, size should be compared with habits and the local environmental conditions of the populations, and at various times of year, as well as geography. But in this paper I am correlating size with geography, and mentioning a few of the possibly correlated environmental factors of the breeding ranges.

WING, WEIGHT, AND GEOGRAPHY

One aspect of this is one of the most widely quoted ecological rules, often stated as: Within a species, birds from higher latitudes are larger. It seems to have application, but is by no means the whole story, its applicability varying in different parts of the continent. Another aspect which may be important is the relatively lighter weight of some western populations of widespread species. As might be expected, there are exceptions to both generalizations.

Eastern North America.—Increase in wing length and weight with increase in latitude is shown by ten species as follows:

(a) nine species in eastern United States, eight of them listed in Table 1, and the United States population of the Sandhill Crane (Table 2); and

TABLE 1

COMPARISON OF WING LENGTHS AND WEIGHTS OF GEOGRAPHICALLY SEPARATED BIRDS

Species and Location	Wing Length (mm.)		Weight (grams)	
	♂	♀	♂	♀
Hairy Woodpecker (*Dendrocopos villosus*)				
Southeastern United States	113	112	(1) 58	(2) 50
Northeastern United States	120	119	(11) 73	(12) 63
Downy Woodpecker (*Dendrocopos pubescens*)				
Southeastern United States	88	88	(1) 23	(4) 21
Northeastern United States	94	94	(23) 26	(19) 28
Carolina Chickadee (*Parus carolinensis*)				
Southeastern United States	59	55	(5) 9	(4) 8
Northeastern United States	64	61	(13) 10	(24) 9
Tufted Titmouse (*Parus bicolor*)				
Southeastern United States	77	76	(5) 20	(2) 18
Northeastern United States	80	77	(17) 22	(12) 20
Blue Jay (*Cyanocitta cristata*)				
Southeastern United States	126	121	(4) 78	(6) 71
Northeastern United States	137	134	(10) 88	(7) 86
Red-winged Blackbird (*Agelaius phoeniceus*)				
Southeastern United States	112	92	—	(4) 35
Northeastern United States	120	98	—	(7) 43
Common Grackle (*Quiscalus quiscula*)				
Southeastern United States	133	119	(8) 108	(6) 79
Northeastern United States	144	126	(23) 120	(9) 101
Cardinal (*Richmondena cardinalis*)				
Southeastern United States	90	84	(4) 37	(1) 32
			(7) 39	(10) 38
Northeastern United States	94	90	(16) 45	(13) 42
			(30) 43	(10) 44

The data on weight are from Amadon, 1944; Hartman, 1955; and Norris and Johnston, 1958; the data on wing length from standard taxonomic sources. Averages only are given. Numbers in parentheses are numbers of specimens.

TABLE 2

COMPARISON OF WING LENGTHS AND WEIGHTS OF SPECIES NESTING ON THE ARCTIC BARRENS

Species and Location	Wing Length (mm.)		Weight (lbs.)	
Canada Goose (*Branta canadensis*)				
Mid continent	410–550		6 –18	
Arctic barrens	350–480		4 – 5	
Snow Goose (*Chen hyperborea*)				
No. Alaska to So. Baffin Island	387–450		4 – 6½	
No. Baffin Island to No. Greenland	425–485		5½–10½	
	♂	♀	♂	♀
Sandhill Crane (*Grus canadensis*)				
Florida, etc.	501	477	(3) 10	(1) 8¼
Mid continent, etc.	539	533	(7) 11⅞	(4) 9½
Arctic barrens, etc.	468	447	(11) $9\frac{13}{16}$	(10) $8\frac{13}{16}$

Data from Delacour (1954) and Walkinshaw (1949). Numbers in parentheses are numbers of specimens.

TABLE 3

COMPARISON OF WING LENGTHS AND WEIGHTS OF BIRDS FROM THREE WIDELY SEPARATED AREAS IN THE UNITED STATES

Species and Location	Wing Length (mm.)		Weight (grams)	
	♂	♀	♂	♀
Hairy Woodpecker (*Dendrocopos villosus*)				
Southeastern United States	113	112	(1)58	(2)50
Northeastern United States	120	119	(11)73	(12)63
Western United States (Nevada)	133	131	(1)74	(3)61
Downy Woodpecker (*Dendrocopos pubescens*)				
Southeastern United States	88	88	(1)23	(4)21
Northeastern United States	94	94	(23)26	(19)28
Western United States (Nevada)	99	100	(6)26	(2)25
White-breasted Nuthatch (*Sitta carolinensis*)				
Southeastern United States	87	85	—	—
Northeastern United States	90	88	(20)20	(21)20
Western United States (Nevada)	90	88	(5)16	(2)16
Loggerhead Shrike (*Lanius ludovicianus*)				
Southeastern United States	98	97	(12)48	(6)47
Western United States	99	98	(20)48	(14)50
Lower California	101	—	(7)45	—
Rufous-sided Towhee (*Pipilo erythrophthalmus*)				
Florida	80	76	(11)44	(4)36
Georgia, etc.	85–87	80–83	(11)45	(6)44
Northeastern States	87	83	(44)41	(10)38
California (Hastings)	87		(13)38	

Data on weight from Linsdale (1936), Miller (1931), Hartman (1955), Norris and Johnston (1958), and Davis (1957). Wing length is from standard taxonomic sources. Numbers in parentheses are numbers of specimens.

(b) one species, the Snow Goose, of the Arctic barrens (Table 2).

Exceptions to this are three in number, as follows:

(a) the Rufous-sided Towhee of the Eastern United States, which is longer-winged but lighter in weight in the Northeast (Table 3); and

(b) the Canada Goose and the mid-continent and northern populations of the Sandhill Crane (Table 2).

For comparison, Chapman (1912) listed 27 species which had longer-winged northern subspecies in eastern North America, and seven with shorter-winged northern subspecies.

Western North America.—Both environmental factors and geographical variation in the mountainous western part of the continent are complex.

As one might expect, the detailed studies of jays by Pitelka (1951), shrikes by Miller (1931), juncos by Miller (1941), and nuthatches by Norris (1958), indicate that latitude and size variation do not correlate well.

Eastern and Western United States.—In Table 3, I have listed five species in which populations from the western United States are relatively lighter in weight, compared with wing length, than populations from the eastern United

TABLE 4

COMPARISON OF WING LENGTHS AND WEIGHTS BY SUBSPECIES

Subspecies and Location	Wing Length (mm.)		Weight (grams)	
	♂	♀	♂	♀
Warbling Vireo				
(*Vireo gilvus swainsoni*) (Nevada)	67	66	(10) 11	(10) 11
(*V. g. gilvus*) (Kansas on migration)	73	70	(12) 15	(5) 16
Solitary Vireo				
(*Vireo solitarius cassinii*) (Nevada)	72	72	(8) 15	(6) 14
(*V. s. solitarius*) (Maine)	75	—	(5) 16	(5) 16
Scrub Jay (♂ only)				
(*Aphelocoma coerulescens*)				
Florida	115	—	(2) 78	—
12 western subspecies	118–143	—	79–125	—

Data from Linsdale (1936), Hartman (1955), Tordoff and Mengel (1956), and Pitelka (1951). Numbers in parentheses are numbers of specimens.

States. In two of these (Downy and Hairy Woodpecker), the wing length of the western birds is greater, but the weight is about the same. In two others (nuthatch and towhee), the wing is the same but the weight is less in the west; in the shrike the Lower California bird has a lighter weight.

In two species of vireos (Table 4), the wing length and the weight are both less in the two western populations.

In the Scrub Jay (Table 4) the Florida population is both shorter-winged and lighter in weight than any of the western populations.

That is, for eight species, one is a case of smaller wing and lighter weight in the east; two are cases of smaller wings and lighter weight in the west, and five are cases in which the western populations are relatively lighter-bodied.

WING LENGTH CORRELATIONS

There are other cases of greater wing length at both higher and lower latitudes in the eastern part of North America, and of birds with larger wings in the west and southwest, but I have no weight data. However, there are two other categories which I want to mention in regard to variation in wing length, as similar correlations may be found in weight variation.

Wing Length and Altitudes.—There seem to be no clearly demonstrated altitudinal subspecies in North America. The mountain subspecies, of which we have a number, are latitudinal representatives as well.

Marshall (1957: 57–58), in his studies of Arizona birds, has shown that what have been considered altitudinal subspecies there are capable of another interpretation, i.e., a latitudinal one.

This does not mean, however, that there is no evidence for increase in wing length with increase in altitude in the New World, as has been stated by some

TABLE 5

WING LENGTHS OF TWO GROUPS OF VIREOS ON CARIBBEAN ISLANDS

	VIREO OLIVACEUS Superspecies	VIREO GRISEUS Superspecies
	Wing, male only 67–82 mm.*	Wing, male only 55–66 mm.*
Bahamas	80	64
Florida Keys	80	—
Tortugas	—	63
Old Providence	—	61
Cozumel	—	62
Grand Cayman	74	—
Cuba	—	56
Jamaica	—	58
Hispaniola	83	—
Puerto Rico	—	65
St. Kitts	80	—

Data from Hamilton (1958).
*Range in averages of continental populations.

authors. Traylor (1950) has presented good evidence for this type of geographical variation in birds in the mountains of Bolivia.

Wing Length Irregularity in the West Indies.—The data Hamilton (1958) gives for two West Indian vireos, *V. olivaceus* (superspecies) and *V. griseus* (superspecies), are very interesting as indicating no obvious pattern to the variation in wing length. Not latitude, longitude, size of island, humidity, or temperature seem to fit the pattern of variation. As only one of the 11 islands concerned has both species, it seems that interspecific competition is not concerned. On the Bahamas where both occur, in each case a large but not the largest race of each species occurs.

Hamilton (1958: 334) says that *Vireo olivaceus* and *V. griseus* show the tendency for insular populations to have "greater wing length and relatively longer bill length (see Murphy, 1938)."

A survey of the tabular material on wing length, Table 5, does not support this aspect of the statement, nor does Murphy (1938) discuss wing length, in the paper cited.

Rather, these island vireos seem to be cases of the irregularity which is conspicuous in island populations. Similar irregular variation may account for some of the variation in series of continental populations.

CHARACTER GRADIENTS

Characters sometimes change gradually, giving a cline. The measurements for the Hairy Woodpecker for the eastern United States (Table 6) is a good illustration of a character gradient or cline.

But the term cline, and especially stepped cline, is often used when the

TABLE 6

CLINE IN WING LENGTH FROM NORTH TO SOUTH

Species and Location	Wing Length (mm.)	
	♂	♀
Hairy Woodpecker (*Dendrocopos villosus*)		
Maine and New Brunswick	125–129	[illegible]
New York and Pennsylvania	119–122	116–120
Maryland and District of Columbia	119	—
Virginia	117–118	118
North Carolina	119	115
South Carolina	116	113
Georgia	113	113
Florida	113	111

Data from Ridgway (1914:202–203).

characters are uniform over a considerable area, then suddenly change to another. These cause one to wonder if some other than environmental factors may not be at work. The towhees (Table 3) are a case in point, in which the wing from New England to Georgia averages about 87 mm.; in Florida it averages 80 mm. (males only), and it is especially interesting that the change in weight does not occur in the same place as does that in wing length.

Another case is that of the Carolina Wren in which the wing length of the male averages 62 mm. in the peninsula of Florida, but only 60 mm. from northern Florida to New England (Lowery, 1940). In such cases, the question arises if the terms character gradient or cline are properly used for the whole geographical range, when such a small proportion of it actually shows a cline.

SPECIES SHOWING TWO TYPES OF VARIATION

I have wing and weight data on three species which, depending on the area the samples come from, show two types of variation. The Downy and Hairy Woodpeckers show increase in wing length and weight from south to north in eastern North America, but are relatively lighter in weight in the western part of the country (Table 3). Two types of change with latitude are shown by the Sandhill Crane. The southern birds (Florida) are medium in wing and weight; the mid-continent birds are large (increase in size with latitude); the northern birds are smallest (decrease in size with latitude), see Table 2.

DISCUSSION OF CORRELATIONS

The above correlations are based on facts. That the geographical factors are the direct, causal factors is improbable. Rather, the causal factors are probably correlated with the geography.

The following correlations are to be considered here, though others, such as interspecific competition and migration, could play a part:

Temperature.—The classical increase in size, both wing length and weight, in colder parts of the species range, is evident in eastern North America; 10 cases of positive correlation; three cases of exceptions.

Aridity Effect.—This, as Hamilton (1958: 320–327) proposed it, has no factual basis whatever. On the basis of longer wing length of populations from the western part of North America, he postulated a greater body weight, and then discussed the physiology of greater weight in more arid regions. But, he had no weights. Outside the vireos, he presented wing lengths for only four species: Downy Woodpecker, White-breasted Nuthatch, Loggerhead Shrike, and Cardinal. Of these, I have presented weights as well as wing lengths for the first three, and the western birds are not heavier than eastern populations, though their wing lengths are indeed longer in two cases, and all three are relatively lighter in weight.

Habitat Effect.—Both Miller (1931: 102–105) and Pitelka (1951: 366) have suggested that where the interstices of the habitat are smaller, one would expect birds to fly less and to be smaller-winged, with heavier bodies; openness of habitat may correlate with more space in which the bird may fly, and greater need for flight, and result in birds being longer-winged, or relatively longer-winged. I have pointed out elsewhere (Rand, 1961) that between species, the birds that fly most are relatively longer-winged and lighter in weight. In the present paper I have given data on several species in which this may apply to western populations.

Randomness of Variation (Lack of correlations).—In the complexity of adaptations, one would expect some birds to adapt in other ways than by size. They have to be some size, and they may exist in spite of their precise size.

SUMMARY AND CONCLUSIONS

The complexity of variations and the factors that bring them about are so great that we are fortunate in being able to see partial correlations over limited areas, and being able to use subspecies names and ecological rules to codify part of our knowledge.

The only effect for which there is evidence enough to be convincing is that decreasing temperature correlates with larger wing and weight (this is in accord with Bergmann's rule), and this only in eastern North America.

Suggestive is the evidence that relatively longer-winged (or lighter-bodied) western representatives of birds may occur in the more open habitats there (which last may be correlated with aridity), where more flying is involved in the daily life of the bird.

This points up the fact that wing length is not always an indicator of body

weight within a species, especially when birds from quite different environmental conditions are compared.

More than one factor could be in operation at one time, working in different directions, canceling or modifying each other.

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CHICAGO NATURAL HISTORY MUSEUM, CHICAGO 5, ILLINOIS, 5 FEBRUARY 1960

NEW LIFE MEMBER

Jayson A. Walker, of Waterloo, New York, has been an active member of the Society since 1949. He is especially interested in the banding and photographing of birds, but is also interested in the study of flowering plants, reptiles, and amphibians. Mr. Walker is also a member of the AOU, Federation of New York State Bird Clubs, and the Eastern Bird Banding Association. We welcome him as a new life member of the Wilson Ornithological Society.

INTRASPECIFIC VARIATION IN PASSERINE BIRD SONGS

DONALD J. BORROR

THE vocalizations of birds are of interest to ornithologists because of the role they play in behavior, and because of their value in species recognition. These vocalizations are subject to intraspecific variation, but the accurate study of this variation involves somewhat different techniques than are involved in the study of morphological variation. Developments in recording and sound-analyzing equipment in the last fifteen years or so have made it possible to study variation in bird vocalizations with a degree of accuracy comparable to that of morphological studies.

My colleagues and I at Ohio State University have been making tape recordings of bird songs since 1948, and we now have over 4,400 recordings, representing nearly 250 species. A great many of these have been analyzed by means of a sound spectrograph, and while we may not have as many recordings as we would like, to make a thorough study of variation in any species, perhaps enough recordings have been obtained and analyzed to present some general points regarding the intraspecific variation in the songs of birds in the order Passeriformes.

An individual bird may produce a variety of sounds; we are concerned here with the particular vocalizations of passerine birds that are called *songs*. Song may be defined as the vocalizations, usually given only by the male and usually more complex in character than the bird's various call notes, which appear to have one or more of three principal functions: (1) to advertise the presence of the male, (2) to attract a female, and (3) to repel other males of the same species. The distinction between song and other vocalizations is not always sharp, partly because the songs of some birds may be of a relatively simple character and not very different from the bird's other vocalizations, and partly because the exact function of many vocalizations is not clearly understood. Most of the songs discussed in this paper are termed advertising or territorial songs by many ornithologists.

Theoretically, many sorts of variation might occur in passerine song. Song might vary in an individual bird, in different individuals of a local population, and/or in the birds of different (geographically separated) populations. The songs of an individual might vary with age, time of day, season of the year, the presence of other birds, or other factors. Different individuals, either in a local population or in geographically separated populations, might sing songs of different patterns, or show different preferences for a limited number of song patterns.

SONG DEVELOPMENT IN THE INDIVIDUAL

A male passerine bird usually begins to sing when it is several months old, and thereafter sings principally (or solely) during the breeding season. In species where different individuals sing essentially the same song it is probable that the song patterns are largely hereditary, but in species where different individuals sing somewhat different songs (the situation in the majority of passerine birds), it is probable that at least some features of the songs are learned by listening to other birds. The role of learning in song acquisition has been pointed out by a number of investigators, including Thorpe (1951, 1954, 1956, 1958*a*, 1958*b*), Koehler (1951), Poulsen (1951, 1958), and Lanyon (1957, 1960).

The early season singing of birds whose song patterns are at least in part learned is somewhat atypical; the patterns are erratic and somewhat abortive, and the birds sound as though they were trying to decide just what patterns to sing, and to perfect their singing technique. Later in the season, as the bird perfects its song patterns, little of this type of singing is heard. Many passerine birds that sing during their migration sing songs that are a little different (e.g., more variable, with the patterns less well defined) from the songs sung by these birds on their nesting grounds; such birds are probably in the "perfecting" stage of their song development. Once the bird's song patterns are perfected they appear to be largely fixed for the rest of the bird's life; there appears, based on my study of the songs of a number of individual birds over periods of two to four years, to be relatively little variation from year to year in the song patterns of a given individual.

Our collection of bird recordings contains a number in which the songs are very atypical for the species, and closely resemble the songs of another species. Some birds rather regularly mimic the songs and calls of other species (the Mockingbird and Starling are well known examples), but occasionally other birds—species not generally considered mimics—will do this. Tasker (1955), for example, reports a Chipping Sparrow with the song of a Clay-colored Sparrow, and Hulme (1950) reports a Chaffinch mimicking the song of a Hedge Sparrow. Among our recordings of such atypical mimicry are recordings of a Rufous-sided Towhee and a Bachman's Sparrow singing Field Sparrow songs, a Field Sparrow singing a song similar to that of a Prairie Warbler, and a Red-eyed Vireo singing towhee-like songs. I have seen a Blue Jay that was exposed since it left the nest only to Robin song, and which sang a robin-like song. It seems likely that these cases of mimicry are the result of the bird learning its song from another species.

LOCAL VARIATION

Different species of passerine birds differ in the amount of variation in the songs of a given individual and in the songs of different individuals. The

TABLE 1

AN OUTLINE OF THE INTRASPECIFIC VARIATION IN THE ADVERTISING SONGS OF PASSERINE BIRDS

Songs of a Given Individual	Songs of Different Individuals			
	Of the Same Pattern	Of a Few Different Patterns	Of Many Different Patterns	Of Many Different Patterns
		Much Overlapping	Some Overlapping	Little or No Overlapping
Of One Pattern	Least Flycatcher Traill's Flycatcher*	Savannah Sparrow Grasshopper Sparrow	Yellowthroat Chipping Sparrow Slate-colored Junco	
	White-breasted Nuthatch	Ovenbird Kentucky Warbler White-throated Sparrow		
Of a Few Patterns	Wood Pewee Phoebe Traill's Flycatcher*	Black-throated Green Warbler Parula Warbler	White-eyed Vireo	Indigo Bunting Field Sparrow Vesper Sparrow
	Blue-winged Warbler		Tufted Titmouse Cerulean Warbler American Redstart	
Of Many Patterns			Rufous-sided Towhee Carolina Wren Cardinal Bachman's Sparrow	Wood Thrush Hermit Thrush Song Sparrow Lark Sparrow

* The reason for Traill's Flycatcher appearing in two places in this table is discussed on p. 74.

types of intraspecific variation found in the advertising songs of a number of passerine birds are outlined in Table 1. This table does not include species that sing more or less continuous songs, such as the Catbird, Brown Thrasher, and Red-eyed Vireo, because the songs of these species have not yet been studied in sufficient detail; such species would probably fit somewhere in the lower right-hand part of the table. Most passerine birds that sing short isolated songs (in contrast with more or less continuous songs) would probably fit into one of the four top center squares. Most nonpasserine birds probably fit in the left-hand square in the top row.

The songs of some species consist of a definite sequence of notes and phrases, and the different songs of a particular pattern sung by a given individual are practically identical; in other species, where all or part of the song consists of a series of similar notes or phrases, different songs of a particular

pattern sung by a given individual may differ in the number of such notes and phrases. In the squares of Table 1 containing a broken line, the different songs of a particular pattern sung by a given individual of the species above the broken line are practically identical, but in the species below the broken line the number of notes or phrases in different parts of the song may vary. In squares with no broken line, the different songs of a particular pattern sung by a given individual of all the species listed are subject to variation in the number of notes or phrases they contain.

In some species of passerine birds (for example, the species listed in the top row of the table) the songs of a given individual are all of the same pattern; in others (the species listed in the middle row of the table) each individual may sing songs of two to five different patterns; in still other species (those listed in the bottom row of the table) each individual may sing songs of six or more different patterns.

The greatest amount of variation in the songs of a given individual was found in the species listed in the bottom row of Table 1. The maximum number of song patterns in our recordings of a single individual is 8 for a Rufous-sided Towhee (Borror, 1959*a*), 11 for a Cardinal, 13 for a Song Sparrow, 13 for a Hermit Thrush (Borror, 1960), 18 for a Wood Thrush (Borror and Reese, 1956), 22 for a Carolina Wren (Borror, 1956), 37 for a Bachman's Sparrow, and 58 for a Lark Sparrow. Variation within patterns occurred in all these species. The songs of a given pattern in the Song Sparrow, for example, may vary in the number of phrases of a given type in different parts of the song, in the presence or absence of certain notes or phrases, in where (along a certain sequence of notes and phrases) the song ends, and/or in the particular types of phrases with which the song begins or ends; the variation in Song Sparrow songs is such that the delimitation of patterns is occasionally somewhat arbitrary. In the 462 songs we have recorded from one Maine Song Sparrow, which had 13 distinct song patterns, there were 187 different songs.

In some species (those listed in the left-hand column of Table 1) the songs of different individuals are of the same pattern, with only slight individual differences (see Figs. 1, 4, and 5). In other species (those listed in the second column of the table) the songs of different individuals are occasionally of different patterns, but our recordings do not contain more than 12 different song patterns for any of these species; it is quite common ("much overlapping" is the way this is described in the table) to hear different individuals singing songs of the same pattern. In still other species (those listed in the third column of the table) the songs of different individuals are usually different, and our recordings contain more than 12 patterns for each of these species; it is only occasionally that one hears different individuals singing songs of the same pattern. In still other species (those listed in the right-hand

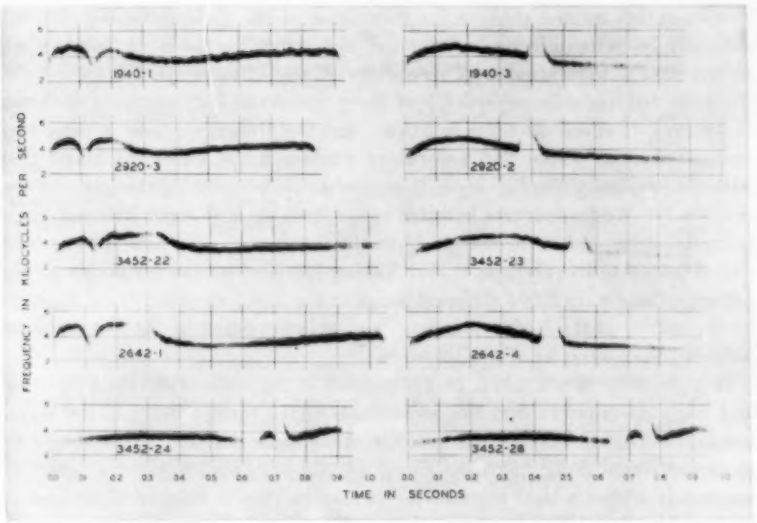

FIG. 1. Audiospectrographs* of Wood Pewee songs. The four upper graphs on the left are of *pee-ah-wee* songs, the four upper graphs on the right are of *peee-ah* songs, and the two graphs at the bottom are of *aaah-didi* songs; 3452 is a recording of the daybreak song, and the other recordings are of daytime songs. 1940, New Albany, Ohio, 26 May 1956; 2920, Lincoln Co., Maine, 30 June 1957; 3452, Bloomington, Indiana, 1 June 1958; 2642, Franklin Co., Ohio, 15 May 1957.

column of the table), our recordings of which contain many different patterns, one rarely if ever hears different individuals singing songs of the same pattern.

The greatest amount of variation in the songs of a given species was found in the birds listed in the right-hand column of Table 1. Our recordings do not contain any instance of two different birds singing songs of the same pattern in the cases of the Indigo Bunting, Vesper Sparrow, Wood Thrush, Hermit Thrush, or Lark Sparrow, and only a few such instances in the cases of the Field Sparrow and Song Sparrow. The different patterns of Field Sparrow songs are fairly similar, and the delimitation of these patterns is somewhat subjective; with a fairly strict delimitation of patterns, only about 2 per cent of our Field Sparrow recordings represent cases of a given pattern being sung by different individuals. The song patterns of the other

* The recordings from which the song graphs in this paper were made are in the collection of recorded animal sounds of the Department of Zoology and Entomology, Ohio State University. I made them all with a Magnemite recorder, Model 610-E, using a tape speed of 15 inches per second; the graphs were made with a Vibralyzer. The first of the two numbers on each graph is the number of the recording, and the second (unless otherwise indicated) is the song in the recording, from which the graph was made.

species in this column differ more than those of the Field Sparrow, and can generally be more objectively delimited, but except for the Song Sparrow we do not have a large number of recordings of any of these species.

Of the 501 recordings we have of Song Sparrows, 356 are from 46 birds in an area of about 40 acres in Maine, and were obtained over a period of several seasons. These 356 recordings contain 2,868 songs, of about 200 patterns (the exact number depends somewhat on how strictly the patterns are delimited). We have over a hundred songs from each of eight different birds from this area, and in these eight birds the number of song patterns per bird varied from 6 to 13 (average, 8.25). Taking into account the variations within patterns, there were 1,494 different songs in the 2,868 recorded from these 46 birds; only 6 of the 1,494 variations, and about a dozen of the two hundred patterns, were sung by different birds.

It is probably very unusual, except possibly in the cases of the Field Sparrow and Song Sparrow, to find two individuals of the species listed in the right-hand column of the table singing songs of the same pattern. Cases of two or more individual Song Sparrows singing songs of the same pattern probably occur only within a local population. It may be that in some of these species no two birds ever sing songs of the same pattern.

There is a great deal of variation in song pattern in the species listed in the third column of the table, even though our recordings contain a number of instances of a given pattern being sung by different individuals. For example, we have 138 different song patterns in 113 Cardinal recordings, 127 patterns in 12 Bachman's Sparrow recordings (seven birds), 93 patterns in 71 Rufous-sided Towhee recordings (Borror, 1959*a*), 45 patterns in 84 Yellow-throat recordings, and 36 patterns in 86 Chipping Sparrow recordings.

GEOGRAPHIC VARIATION

Any bird observer with a critical ear for patterns in bird songs will note that the song patterns of many passerine birds differ somewhat in different areas, but these differences have been critically studied in only a few species. "Local dialects" have been described for the Chaffinch by Marler (1952), Poulsen (1958), and Thorpe (1954). Lanyon and Fish (1958) have discussed the geographic variation in the songs of the Western Meadowlark, and I have published some data on the geographic variation in the songs of the Carolina Wren (Borror, 1956), the Rufous-sided Towhee (Borror, 1959*a*), and the Chipping Sparrow (Borror, 1959*b*). It may be of interest to mention here a few additional examples, based on my studies.

Bachman's Sparrow (*Aimophila aestivalis*).—The songs of this species typically consist of one or two introductory notes followed by a trill; the introductory notes are relatively long and usually steady in pitch, and the

TABLE 2

CHARACTERISTICS OF THE TRILL IN THE SONGS OF SEVEN BACHMAN'S SPARROWS

Character		3 birds in Ohio	4 birds in Florida
Phrase Length* (in sec.)	Range	0.032–0.220	0.040–0.230
	Average	0.124	0.166
Number of Phrases	Range	1–20	4–11
	Average	8.94	7.67
Number of Different Phrase Types	1-noted	12	2
	2-noted	34	15
	3-noted	22	23
	4-noted	1	12
	Total	69	52
Average number of notes per phrase		2.17	2.87
Total number of songs recorded		447	81

* Phrase length is the length of time from the beginning of one phrase to the beginning of the next; the reciprocal of this figure is the number of phrases per second.

trill consists of a rapid series of similar phrases. A given bird may sing songs of a number of different patterns, each pattern consisting of a characteristic introduction and type of trill phrase. In recordings of seven individuals of this species I studied, three from Ohio (*A. a. bachmani*) and four from Florida (*A. a. aestivalis*), and containing 528 songs, there were 127 different song patterns (37 in the songs of one Ohio bird). Several song patterns occurred in the songs of two or three birds in the same state; there was no pattern that occurred in the songs of both an Ohio and a Florida bird. Data on certain features of the trill in the Ohio and Florida songs are given in Table 2; these data indicate that (1) the trill phrases are uttered more slowly, on the average, by the Florida birds than by the Ohio birds (about six per second in Florida songs and eight per second in Ohio songs), (2) the trills in the Florida birds contain, on the average, fewer phrases than those of the Ohio birds, and (3) the trill phrases of the Florida birds contain, on the average, more notes than those of the Ohio birds. (It might be said that the Florida birds had a "southern drawl.")

Song Sparrow (*Melospiza melodia*).—The songs of this sparrow consist of a series of different phrases (mostly 1- to 4-noted), and usually a trill; many of the notes are buzzy. The song begins with a series of similar phrases, either two to four (rarely one or five) uttered at a constant rate, or four to 20 that increase in tempo. A given bird has a vocabulary of a large number of notes and phrases, and these are variously combined to produce up to a dozen or more different song patterns; the different patterns of a given bird

are often quite different. The songs of a given pattern may vary, as noted above (p. 60).

Our Song Sparrow recordings include 388, of some 70 birds, from Maine (*M. m. melodia*); 356 of these are of 46 birds in an area of about 40 acres, and the rest are from varying distances up to 160 miles from this 40-acre area. The vast majority of the songs of the birds in the 40-acre area contain notes and phrases that occur also in the songs of other birds in this area; the songs of birds outside this area contain fewer notes and phrases like those of birds in the area, and the farther away from this area the bird is the fewer the similarities in notes and phrases. In the songs of the Ohio Song Sparrows (*M. m. euphonia*) that have been analyzed to date (of 66 birds, and containing 501 songs of 110 different patterns), the phrases are nearly all different from those of the Maine birds.

Song Sparrow songs are of two general types, those beginning with two to four (rarely one or five) similar and equally spaced phrases, and those beginning with four to 20 similar phrases that increase in tempo; most song patterns can be readily classified into one of these two categories. Songs of the first type were much more common, making up 83.8 per cent of the Ohio patterns and 86.7 per cent of the Maine patterns (these differences in percentage are not significant).

A Song Sparrow apparently has an inborn tendency to sing songs of two general types, but it learns its phrases by listening to other, nearby Song Sparrows. As a result, the songs of different birds in a local population contain similar notes and phrases (but usually arranged differently), while the songs of birds in separated populations contain different phrases. The farther away two populations are, the less likely they are to use similar phrases in their songs.

Cardinal (*Richmondena cardinalis*).—To date I have analyzed 113 recordings of Cardinal songs (containing 946 songs from 100 birds in eight states). These songs consist of 1–43 loud, clear, whistled phrases uttered at rates of 0.9 to 9.0 phrases per second. The songs studied contained 82 different types of phrases (plus a buzzy trill), of which 31 were one-noted, 37 were two-noted, 11 were three-noted, 2 were four-noted, and 1 was five-noted. Cardinal songs may be one-parted, that is, all the phrases alike and uttered at a uniform rate (except possibly the first two or three phrases, which are often slower), or they may contain up to five parts (with the phrases of one part different from those of the next part). The songs are occasionally followed by a buzzy trill (a series of abruptly up-slurred notes, 27–31 per second) that may last up to 1.5 seconds. By giving each phrase type a number, any given song pattern could be represented by one to five numbers (one number for one-parted songs, two for two-parted songs, and so on). The songs of a given bird

may vary in pattern (up to 11 in one Florida bird), and the songs of a given pattern may vary in the number of phrases they contain. There were 138 different patterns in the songs studied, of which 47 were one-parted, 64 were two-parted, 21 were three-parted, 4 were four-parted, and 2 were five-parted.

It is fairly common to hear two Cardinals in a given area singing songs of the same pattern, but it is less common for birds in different areas (i.e., different local populations, in areas separated by four miles or more) to sing songs of the same pattern. Of the 138 patterns found, however, 18 (14 one-parted and 4 two-parted) were sung by birds in different areas; 4 of these were sung by birds in two different states, and 1 pattern was sung by birds in four different states.

The songs of the Ohio birds, *R. c. cardinalis* (797 songs, of 85 birds, and containing 114 song patterns), contained 68 different phrase types, of which 27 were one-noted, 27 were two-noted, 11 were three-noted, 2 were four-noted, and 1 was five-noted; these phrase types averaged 1.87 ± 0.11 notes per phrase. The songs of the Florida birds, *R. c. floridana* (73 songs, of 8 birds, and containing 20 song patterns), contained 20 different phrase types, of which 7 were one-noted, 11 were two-noted, and 2 were three-noted; these phrase types averaged 1.75 ± 0.14 notes per phrase. Ten phrase types (6 one-noted, 3 two-noted, and 1 three-noted) occurred in the songs of both the Ohio and Florida birds. The phrases of the Ohio and Florida birds contained about the same number of notes.

There was no tendency in the songs studied for the birds in different states to sing songs containing a different number of parts. The song patterns in both the Ohio and Florida birds contained an average of 1.9 parts.

Data comparable to the above have been published for a few other species of passerine birds. It has been shown (Borror, 1956) that there are significant differences in the songs of Ohio and Florida Carolina Wrens (representing *Thryothorus ludovicianus ludovicianus* and *T. l. miamensis*, respectively), principally in the phrase rate and the number of phrases in the song; the songs of Florida birds contained, on the average, more phrases and the phrases were uttered more rapidly than in the Ohio birds (the reverse of the situation in the trill of Bachman's Sparrow, described above). In the Rufous-sided Towhee (*Pipilo erythrophthalmus*) it has been shown (Borror, 1959*a*) that the songs of the two subspecies *erythrophthalmus* and *alleni* differ slightly, while the songs of different individuals of the subspecies *erythrophthalmus* as far apart as Ohio and Maine are not significantly different. Studies of Chipping Sparrow songs (Borror, 1959*b*) have shown that there is a great deal of variation in the songs of different birds, but that there is no significant geographic variation within the subspecies *Spizella passerina passerina*, comparing the songs of Ohio and Maine Birds.

In the passerine songs I studied (all from the eastern part of the United States and Canada), there is evidence that in at least some species the songs of different subspecies may differ slightly; within a single subspecies the variation is principally of the sort that might be described as "local dialects," that is, with the birds of different local populations differing in song patterns, but with no significant geographic trends evident.

DIURNAL VARIATION

Most passerine birds sing more consistently in the early morning hours than in the middle of the day; song is usually at a minimum early in the afternoon, and in many species increases again in late afternoon or evening. This phenomenon has been studied in many species, and is apparently correlated with light intensity (Wright, 1912, 1913; Allard, 1930).

A number of birds sing a little differently at daybreak than during the day, and a few sing a little differently at dusk. Distinctive daybreak songs (also called morning twilight songs) have been described for the Wood Pewee (Allard, 1934; Craig, 1943) and for the Crested Flycatcher and the Scissor-tailed Flycatcher (Nice, 1931). We have recordings of distinctive daybreak singing of the Wood Pewee, Crested Flycatcher, and Acadian Flycatcher. There are undoubtedly many other species that sing somewhat differently at daybreak than during the rest of the day. The situation in the Wood Pewee may serve to illustrate the peculiarities of daybreak song.

In its normal daytime singing the Wood Pewee sings songs of two different patterns, *pee-ah-wee* and *peee-ah* (Fig. 1). These two patterns are sung more or less alternately, at the rate of about six or eight a minute; most birds sing about three times as many *pee-ah-wee* songs as *peee-ah* songs. The bird sings a little differently at daybreak; in addition to the two song types just mentioned, it sings a third type, *aaah-didi* (Fig. 1). These three songs are often sung in a definite sequence, at the rate of about 20 songs a minute. This daybreak song begins about an hour before sunrise and lasts about half an hour.

The special daybreak songs of these flycatchers are undoubtedly influenced by light intensity, but their significance to the birds is not clearly understood.

SEASONAL VARIATION

Song is an aspect of bird behavior associated with the breeding season. It begins in the spring, with the onset of the breeding season, usually at a date characteristic for the species. Saunders (1947) presents data on the beginning of song in the spring for a number of species; these dates vary in a given year for different species, and to some extent (usually not more than a week or two) from year to year in a given species. Some species stop or reduce their singing

during certain parts of the nesting cycle, for example, after mating or when they are feeding young; the Song Sparrow ceases singing when it acquires a mate, and begins again when nest building starts (Nice, 1943:118–119).

Song declines after the breeding season and this decline is usually rather gradual, although some species may stop singing rather abruptly. A number of investigators have presented data on the cessation of song in late summer (Bicknell, 1884, 1885; Fry, 1916; Saunders, 1926, 1938, 1948a, 1948b; Baerg, 1930; Vaurie, 1946; Mehner, 1952); the time of cessation varies in different species, and from year to year (as much as two to four weeks) in a given species. The cause of cessation of singing is probably hormonal; cessation usually occurs with the approach of the postnuptial molt.

Some species begin singing again after the postnuptial molt. In general, those species that change color at the postnuptial molt sing in the fall, but the reverse is not always true (Bicknell, 1884; Saunders, 1948). A few species (for example, the Carolina Wren) may sing every month of the year. The songs sung by some species in late fall or winter are often of a rather primitive type (Saunders, 1948), and probably represent "learning" or "practicing" by immature birds (see the discussion on the development of song in the individual, p. 58).

OTHER VARIATION

It might be presumed that, in birds having a number of different song patterns, the different patterns had different meanings to the birds, or particular patterns were sung only under specific circumstances. This may be the case in some birds, but is probably not the case in others; a given type of song or song pattern may serve all the functions of song mentioned above (p. 57), or different functions may be served by different types of songs.

The normal singing rate of a Song Sparrow singing its advertising song is about four to six songs a minute, and it may sing for several minutes at this rate—either from a particular perch or while moving about and feeding. It will sing songs of one pattern for a while, then change to another pattern for a while, then to another, and so on through all or a part of its repertoire. If recorded Song Sparrow songs, of either this same individual or another individual, are played to a bird on its territory, the bird reacts in a characteristic fashion: its singing rate increases to eight or ten songs a minute, and it shows signs of agitation and hops around the speaker. The particular song patterns it sings under these circumstances are the same ones it sings when it is undisturbed; what is changed by the playback is not the bird's song patterns, but its singing rate. I have observed this reaction of Song Sparrows to playbacks on numerous occasions.

Some birds occasionally utter a very soft song that may or may not be of the same pattern as its normal song; such songs are often called secondary

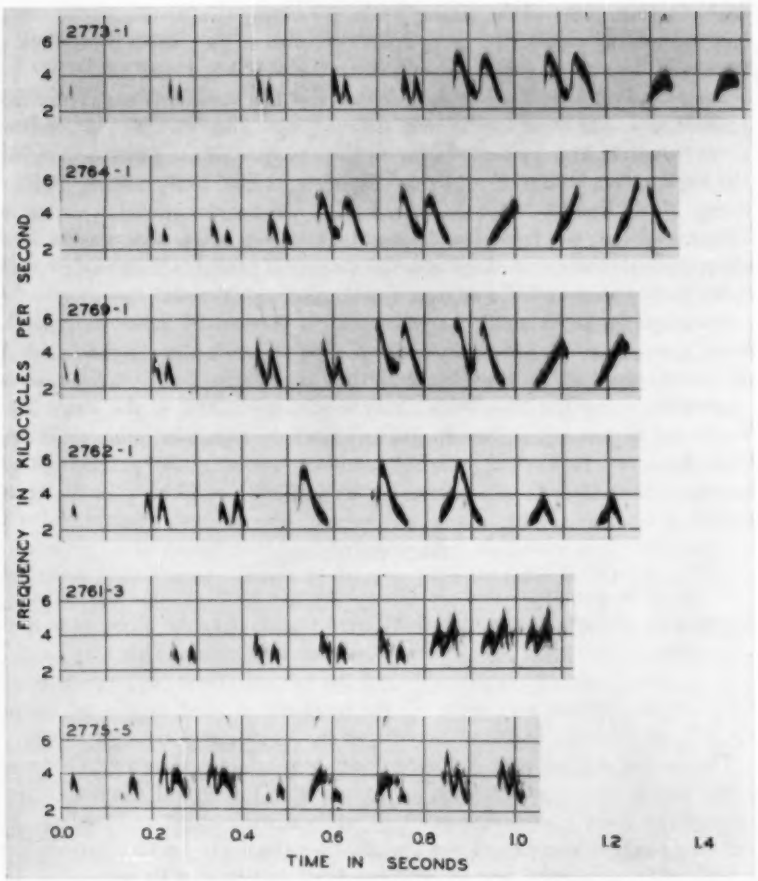

FIG. 2. Audiospectrographs of advertising songs of the Kirtland's Warbler, all from recordings made in Oscoda Co., Michigan, 31 May 1957.

songs, whispering songs, or subsongs (Van Tyne and Berger, 1959:138–139). The significance of such songs is not always clear, but in some species (e.g., the Kirtland's Warbler) these whispering songs appear to function in repelling an intruding male.

A comparison of the advertising and whispering songs of the Kirtland's Warbler is shown in Figs. 2 and 3. The advertising songs of this warbler are of two general types; the songs of one type (the four upper graphs in Fig. 2)

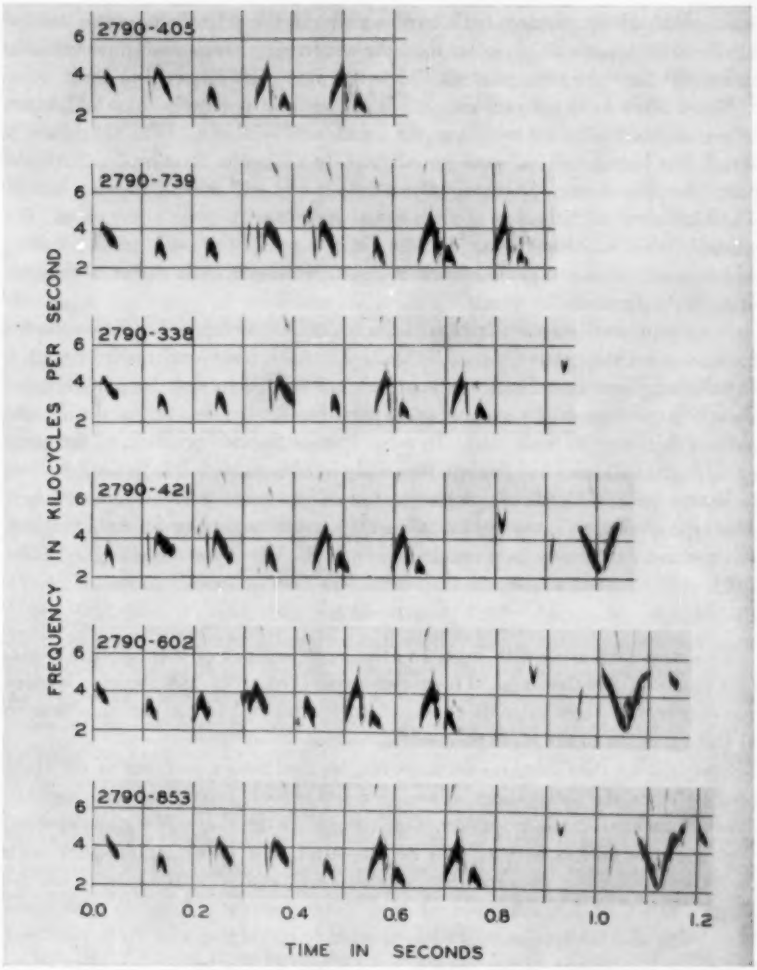

FIG. 3. Audiospectrographs of whispering songs of the Kirtland's Warbler, sung in response to playbacks of the advertising songs on the bird's territory; recorded in Oscoda Co., Michigan, 31 May 1957. The second of the two numbers on each graph is the location of the song in the recording (in minutes and seconds from the beginning).

are somewhat similar in quality and tempo to the songs of the Northern Waterthrush, and the songs of the other type (the two bottom graphs in Fig. 2) are a little like those of a House Wren. Whispering songs (Fig. 3), which

were obtained by playing back a recording of the advertising song on the bird's territory, are much softer than the advertising songs and quite variable in length; they are somewhat similar to the wren-like advertising song.

Many birds have songs which are heard only infrequently, and which are of a somewhat different type than the usual territorial song. The term "flight song" has been used for some such songs (e.g., in the Ovenbird), "twilight song" for others (e.g., in certain flycatchers), and still other terms for others. The biological significance of such songs is known in only a few cases; for example, the "sustained song" of the Grasshopper Sparrow (Smith, 1959), which consists of a typical advertising song followed by a series of buzzes, appears to function in courtship.

Song is primarily a vocalization of the male, but the females of some species may sing occasionally (Nice, 1943:129–132). I have one recording of a female Song Sparrow that was apparently stimulated to sing by playbacks of Song Sparrow songs; its songs were typical for the species, but of a different pattern than any its mate sang. In some species the two sexes sing (the same or different patterns) either simultaneously or alternately. It is not uncommon to hear a pair of Cardinals singing songs of the same pattern (alternately). This type of singing is sometimes called responsive singing, antiphonal singing, or duetting, and occurs in a number of species (Van Tyne and Berger, 1959: 140).

DISCUSSION

Two questions arise with regard to the large amount of intraspecific variation that occurs in the songs of many passerine birds: (1) how the bird student can ever learn to recognize these many song patterns, and (2) the significance of this variation to the birds themselves.

Recognizing Bird Songs.—In most species that sing a number of different song patterns, the patterns are of one or a few general types, and the songs are usually of a characteristic quality. One recognizes the songs of a given species, even patterns he has never heard before, after first becoming familiar with the type(s) of song patterns that species sings and with the quality of the songs. The field identification of bird songs generally involves also some knowledge of what species might be expected to be singing at a given time and place; the importance of this basis of song identification becomes evident when one tries to identify song recordings in the laboratory. If the field observer has an ear for pattern in bird songs, he will eventually be able to recognize individual birds by their songs; this is particularly true for the species listed in the two right-hand columns of Table 1.

Significance of Song Variation to the Birds.—Certain types of songs are known to play a role in courtship or in territorial defense, as we have seen, but the significance to the birds of much of the intraspecific variation in the

advertising songs can for the most part only be guessed. Such data as are available on this point suggest two things, one regarding the ability of the bird to recognize different individuals of its own species, and the other regarding the role played by song in bird speciation.

Individual Recognition.—The advertising songs of an individual Ovenbird are of one pattern (or phrase type), differing only in the number of phrases in the song. One may occasionally find different Ovenbirds with identical phrases, but the songs of different individuals are often different (Table 1). Weeden and Falls (1959) have shown that an individual Ovenbird can distinguish between the songs of different individuals of their species, and can recognize the songs of particular individuals (their neighbors); they react more strongly to songs of nonadjacent birds than to songs of their neighbors. This is apparently a mechanism that reduces strife between birds in adjacent territories once the territorial boundaries are established, and enables the bird to recognize (and possibly cope with) the greater danger of encroachment on its territory by "strangers."

The Role of Song in Speciation.—Song in passerine birds often plays an important role in sexual and species recognition; this has been demonstrated in a number of species (Dilger, 1956; Stein, 1958). Certain vocalizations have been shown to play a similar role in many other animals, including fish (Tavolga, 1956, 1958*a*, 1958*b*; and others), amphibians (Blair, 1955, 1956, 1958; and others), and insects (Alexander, 1957; Alexander and Moore, 1958; Walker, 1957; and others). On the other hand, song in some passerine birds is not the principal means of species recognition; for example in the meadowlarks (*Sturnella magna* and *neglecta*) specific recognition is by call notes rather than song (Lanyon, 1957). Because of the role of song in species recognition, variation in song may lead to speciation; the situation in certain flycatchers may serve to illustrate this point.

An interesting feature of some flycatcher songs is the fact that each individual has two types of songs, or song patterns, which it sings more or less alternately, and different individuals of the species have essentially the same patterns. This is the case, for example, in the Wood Pewee, Phoebe, and Traill's Flycatcher.

The Wood Pewee in most of its singing sings songs of two different patterns, *pee-ah-wee* and *peee-ah* (Fig. 1). These two songs are not sung in any fixed sequence, but a bird generally sings about three times as many songs of the first type as the second.

The Phoebe also sings two types of songs more or less alternately. One type, the "buzz" song (Fig. 4), consists of a slurred note followed by a buzz, and the other, the "sputter" song (Fig. 4) consists of a similar slurred note followed by a sputter. The two types of songs are readily distinguishable by

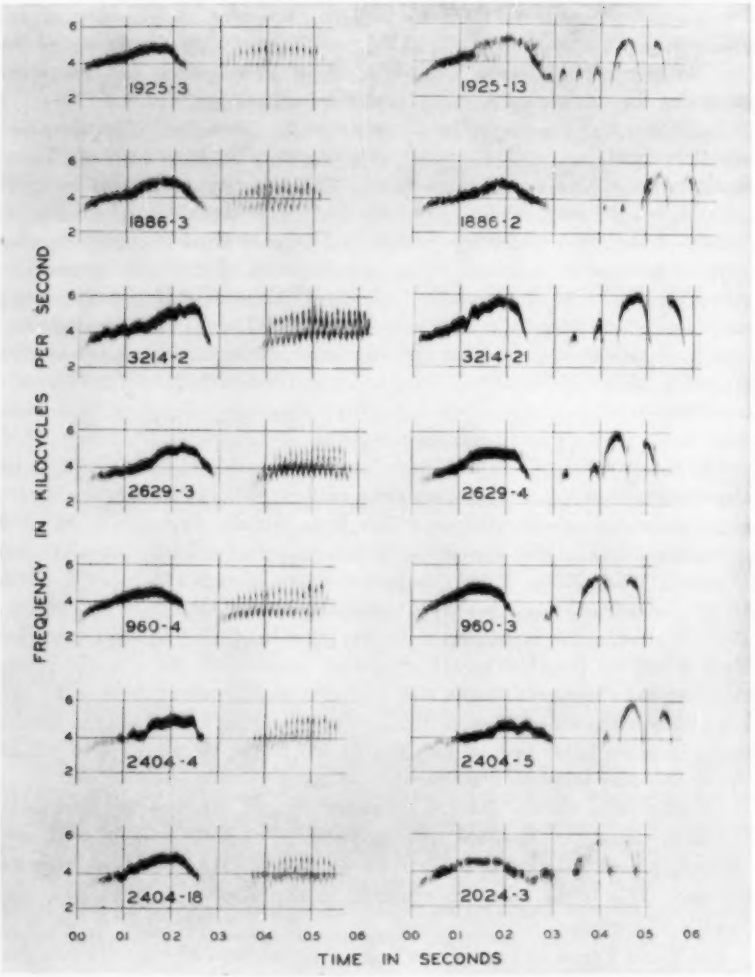

FIG. 4. Audiospectrographs of Phoebe songs; buzz songs on the left and sputter songs on the right. 1925, Columbus, Ohio, 23 May 1956; 1886, Columbus, Ohio, 19 May 1956; 3214, Franklin Co., Ohio, 15 April 1958; 2629, Columbus, Ohio, 13 May 1957; 960, Columbus, Ohio, 26 April 1954; 2404, Columbus, Ohio, 31 March 1957; 2024, Lincoln Co., Maine, 13 June 1956.

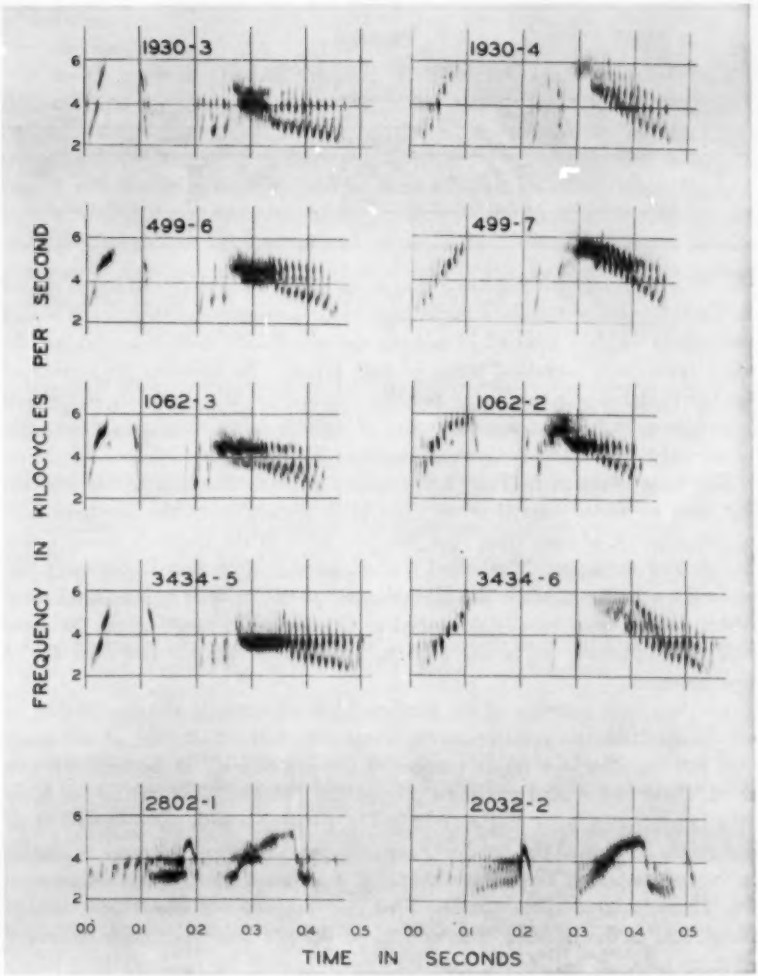

FIG. 5. Audiospectrographs of Traill's Flycatcher songs. The eight upper graphs are of the *fitz-bew* bird, with *fitts-bew* songs on the left and *fizz-bew* songs on the right; the two graphs at the bottom are of the *fee-bee-o* bird. 1930, Columbus, Ohio, 23 May 1956; 499, Columbus, Ohio, 18 May 1953; 1062, Columbus, Ohio, 22 May 1954; 3434, Reynoldsburg, Ohio, 21 May 1958; 2802, Mio, Michigan, 1 June 1957; 2032, Lincoln Co., Maine, 13 June 1956.

TABLE 3

SONG TYPES IN PHOEBE RECORDINGS

Source of Recordings	Number of Recordings	Number of Songs		
		Buzz Type	Sputter Type	Total
Ohio	12	184	99	283
Maine	3	22	30	52
Total	15	206	129	335

ear. The occurrence of these two song types in our Phoebe recordings is shown in Table 3. One of the Ohio recordings (with 3 songs) and two of the Maine recordings (with a total of 21 songs) contained only sputter songs; all the other recordings contained songs of both types. The different proportion of the two song types in the Maine and Ohio recordings is statistically significant (chi square = 9.568); the buzz type of song is more common in the Ohio birds and the sputter type is more common in the Maine birds.

The song situation in Traill's Flycatcher is much like that in the Phoebe, but with an added complication. The birds occurring in the northern part of the country, at least from New England west to the northern Great Lakes region and the upper Mississippi Valley, have a song that is generally described as *fee-bee-o*, while the birds farther south, at least in eastern United States, have a song usually described as *fitz-bew*. The songs of the *fee-bee-o* bird are apparently all of one pattern, but those of the *fitz-bew* bird are of two patterns.

The two song patterns of the *fitz-bew* bird are scarcely distinguishable by ear in the field; they differ in the character of the first part of the song. One pattern (the four upper graphs on the left in Fig. 5) begins with two short, sharp notes, and might be termed the *fitts-bew* song, while the other (the four upper graphs on the right in Fig. 5) begins with an upslurred buzz, and might be termed the *fizz-bew* song; the second part of the song is similar in the two patterns. These two song patterns are sung more or less alternately. Our 16 recordings of the *fitz-bew* bird (all from central Ohio) contain 314 songs, 225 of the *fitts-bew* type and 89 of the *fizz-bew* type; each recording contains songs of both types. Our four recordings of the *fee-bee-o* bird (three from Maine and one from Michigan) contain 37 songs, all of the same type (the two bottom graphs in Fig. 5).

Stein's work on Traill's Flycatcher (1958) indicates that where the two song forms of this bird (*fitz-bew* and *fee-bee-o*) come together in central New York they appear to be distinct species. The morphological differences between the two populations are very slight and overlapping, but the populations differ in certain aspects of nesting behavior; the birds of each population

give a characteristic reaction to songs of their own type, but not to songs of the other population.

It seems probable that the *fee-bee-o* form of this bird evolved from the *fitz-bew* form. A local population of the *fitz-bew* bird in the northeast, which had only the *fizz-bew* song, became isolated from the birds to the south and west—probably during a glacial period of the Pleistocene—and during a period of isolation its song evolved to the *fee-bee-o* type. Now, where the two populations have come together again (in central New York), they behave like distinct species. The Phoebe has probably had much the same history, but the divergence of the northeastern birds from those of the midwest does not appear to have gone as far as it has with Traill's Flycatcher.

SUMMARY

This paper presents an outline of the variation in passerine bird song, based principally on the study of tape recordings by means of a sound spectrograph. Song is the vocalization, usually given only by the male and usually more complex in character than the bird's various call notes, which serves to advertise the male, attract a female, and/or repel other males; most of the discussion in this paper refers to what is usually called the advertising song.

Both inheritance and learning play a part in the acquisition of song patterns by the individual. The early season singing of many species, as the birds are perfecting their song patterns, is somewhat primitive; once these patterns are perfected they are largely fixed for the rest of the bird's life. Occasional individuals in some species apparently learn their song from another species.

Different species of passerine birds differ in the amount of variation in the songs of a given individual and in the songs of different individuals. Individuals of some species have advertising songs of only one pattern, while those of other species may have two to many patterns; 58 patterns were found in the songs of one Lark Sparrow. In some species the songs of different individuals are of the same pattern, but in most species the songs of different individuals may differ. The variation within a species may vary from only a few patterns to a situation in which different individuals seldom if ever sing songs of the same pattern.

Data are presented on the geographic variation in the songs of Bachman's Sparrow, Song Sparrow, and Cardinal (two subspecies in each case). Studies of songs recorded in the eastern United States and Canada indicate that in at least some species the songs of different subspecies may differ; most of the intraspecific variation encountered in the songs from this area might be described as "local dialects," with birds of different areas differing in song patterns, but with few significant geographic trends evident.

Most passerine birds exhibit a daily cycle of singing activity, singing most consistently in the early morning, with the song at a minimum early in the afternoon. Some species sing a little differently at daybreak.

Song is usually associated with the breeding season, beginning in the spring and ceasing in midsummer; some species stop or reduce their singing during certain parts of the nesting cycle, and some may sing after the postnuptial molt.

The same types of song may serve all the functions of song, or different types may serve different functions. Many birds have songs of a different type than the territorial song, that are heard only infrequently ("flight" songs, "twilight" songs, etc.); the

function of these songs is not clear in every case, but in some cases they play a role in territorial defense or courtship. The females of some species sing occasionally, often in response to the male.

The large amount of intraspecific variation in many passerines complicates the problem of the student trying to learn to recognize birds by their songs. Field identification by song is based on the type of song pattern the bird sings, the quality of the song, and a knowledge of what might be expected to be singing at a given time and place. A person with an ear for pattern in bird songs will eventually be able to recognize individuals of many species by their songs; there is evidence that some birds can recognize other individuals by their songs.

Because of the role of song in species recognition, variation in song may lead to speciation; evidence is presented of such speciation trends in certain flycatchers.

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HUNTING AREAS OF THE LONG-EARED OWL

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SEVERAL studies have been made of the feeding habits of the Long-eared Owl (*Asio otus*) (Armstrong, 1958; Geis, 1952; Spiker, 1933; Warthin and Van Tyne, 1922), and have shown this species to feed primarily upon small mammals, particularly the meadow vole (*Microtus pennsylvanicus*). This would indicate that the Long-eared Owl utilizes open, grassy habitats as hunting areas. To my knowledge, however, no study has been made to determine whether the owls are merely feeding in the nearest area that offers a suitable food supply or whether they select some particular habitat (i.e., open, grassy areas).

During the period of September 1957 through September 1958 a study of the ecology of small mammals was conducted in the University of Michigan's Mud Lake Research Area, located in northern Washtenaw County, Michigan. Part of this study consisted of determining the relative abundance of small mammals in all the major habitats in the area. These included most of the typical habitats in the vicinity of the Research Area. A black spruce (*Picea mariana*) stand located approximately in the middle of the Research Area was used as a roosting site by Long-eared Owls. It appeared possible, therefore, that a study of this owl's food habits, as revealed by an examination of the pellets found under the roost trees, might indicate in which habitat the owls were hunting.

I wish to thank Mr. Norman L. Ford for the identification of the bird remains.

DESCRIPTION OF THE STUDY AREA

The Mud Lake Research Area includes about 250 acres. Eight major habitats occur in the area: abandoned field ("old field"), oak-hickory upland, hardwood swamp, spruce swamp, bog mat, birch-aspen swamp, and grass-sedge marsh. These habitats have been described in detail elsewhere (Getz, 1959MS). The habitat features important in regard to this study are discussed below.

METHODS

The basic data revealing the relative abundance of small mammals were obtained by trapping a rectangular portion of each habitat. Seventy-five snap-traps were placed in a grid pattern with a 12-meter interval. Each habitat was trapped for two three-night periods, one in November 1957, and the other in January 1958. In addition to the grid data, a line of snap-traps, with a trap interval of three meters, was placed through each habitat. These transects were trapped for seven nights in September 1958. Monthly live-trapping was con-

TABLE 1

RELATIVE ABUNDANCE OF SMALL MAMMALS IN THE MAJOR HABITATS OF THE MUD LAKE RESEARCH AREA*

Species	Hardwood Swamp	Bog Mat	Spruce Swamp	Spruce Burn	Oak-hickory upland	Old Field	Birch-Aspen Swamp	Marsh
Masked shrew (*Sorex cinereus*)	6	16	11	11	0	1	11	5
Short-tailed shrew (*Blarina brevicauda*)	3	3	1	6	16	8	8	20
White-footed mouse (*Peromyscus leucopus*)	7	1	1	2	30	3	18	3
Deer mouse (*Peromyscus maniculatus*)	0	0	0	0	0	1	0	0
Meadow vole (*Microtus pennsylvanicus*)	0	1	0	0	0	15	0	60
Bog lemming (*Synaptomys cooperi*)	0	3	0	4	0	1	0	5
Jumping mouse (*Zapus hudsonius*)	1	2	0	0	0	1	2	8
Totals	17	26	13	23	46	30	39	101

* Based on 225 trap-nights.

ducted in the marsh and old field from September 1957 through September 1958. These latter two sources of data have been used to modify the results of the grid trapping. A more detailed account of the sampling methods is given by Getz (*op. cit.*).

In September 1958, approximately 125 pellets were collected from beneath the roost trees in the spruce stand. Identifications were made of the remains of the mammals and birds that occurred in these pellets, and from their unweathered condition, it is assumed that the prey were captured during the period of the small-mammal study. Comparisons were made of the food habits of the owls and the distribution of the prey species.

RESULTS

The species (Table 1) and numbers of each recovered from the pellets are as follows: masked shrew, 2; short-tailed shrew, 3; white-footed mouse, 6; deer mouse, 5; meadow vole, 161; bog lemming, 4; Bobwhite (*Colinus virginianus*), 2; Common Grackle (*Quiscalus quiscula*), 1; Evening Grosbeak (*Hesperiphona vespertina*), 2.

As in the previous studies, the meadow vole is by far the most important prey item. The abundance of vole remains and the paucity of remains of other species indicate that the owls were hunting primarily in areas in which voles occurred. The meadow vole was found in only three of the habitats studied

(old field, bog mat, and marsh; Table 1). Since the vole population was very low on the bog mat, and there were very few masked shrew remains in the pellets, this habitat can be eliminated as a major hunting area. Of the two remaining, the old field is the most likely habitat in which the owls hunted. The relative abundance of prey items in the pellets agrees with that of the species present in the old field more than with that of those in the marsh. The presence of remains of deer mice, which occurred only in the old field, is particularly important evidence that this habitat was utilized. The Bobwhite further indicate that the owls were hunting in an upland area rather than in the low, marshy area. Also, one would expect to find the remains of a greater number of short-tailed shrews, as well as a few jumping mice, if the marsh had been utilized to any extent.

The use of the old field rather than the marsh as a hunting area may be related to differences in cover conditions. The vegetation in the marsh consisted of a dense stand of grasses and sedges having an average height of approximately one meter. Even in the winter when the vegetation had fallen over, an almost solid canopy was formed over the surface. The small mammals occupied runways at the base of the vegetation, so it would be difficult for the owls to see, let alone capture them. The vegetation of the old field was relatively sparse and at most ¼-meter tall; over much of the field it was shorter. Although there was some dead grass present, the surface was still partially exposed. The voles would, therefore, be more susceptible to predation in this habitat than in the marsh. The survival rates of the voles inhabiting the old field were less than of those in the marsh (Getz, in press). This may in part be a result of higher predation by such predators as the Long-eared Owl.

When taking into consideration the over-all abundance of small mammals in each habitat, it appears that the owls selected open, grassy areas rather than timbered areas. Excluding the marsh (which had a ground cover shielding the mammals from view) at least two other habitats (birch-aspen and oak-hickory upland) offered a potential food supply as large as or larger than that of the old field. These areas were also nearer the roost than was the old field. Although the surface was relatively free of vegetation, both areas had a considerable amount of underbrush present. The Long-eared Owl, therefore, appears to utilize open, grassy situations as hunting areas even though other types of habitats nearer to their roost may offer a larger food supply.

SUMMARY

Comparisons were made of the food habits of Long-eared Owls and the distribution of small mammals in the habitats surrounding the owls' roost. It was found that the Long-eared Owls fed primarily on the meadow vole, and hunted in an old-field habitat. They apparently did not utilize a near-by marsh, although it contained more voles than the old

field. The use of the old field appears to be related to a lesser amount of cover in this habitat than in the marsh. Timbered areas nearer the roost than the old field and having a greater abundance of small mammals were not utilized. The Long-eared Owls, therefore, apparently prefer open, grassy areas to timbered areas.

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GENERAL NOTES

A wren singing combined House and Carolina Wren songs.—Although the House Wren (*Troglodytes aëdon*) is both a familiar and intensively studied species, there is little or no reported evidence of its engaging in vocal mimicry. The repeated utterance of songs of both House and Carolina Wrens (*Thryothorus ludovicianus*) by a singer apparently belonging to the former species is therefore of interest. The incidents occurred at Bloomington, Indiana, in a suburban yard next to a large undeveloped tract; both House and Carolina Wrens were breeding commonly in the immediate area. The first of the songs was heard on 10 May 1959, at 10 AM. House Wrens had returned to Bloomington on about 18 April, and I had passed the particular spot repeatedly since that date without remarking anything unusual.

During about ten minutes spent within earshot, I heard 30 loud songs, only one of them an unembellished, normal House Wren performance. In all the others a House Wren song, possibly of slightly reduced length, was immediately followed by one, two, or three identical descending Carolina phrases. The one-phrase utterances outnumbered the combined total of the others by at least two to one. The singer was perched in and moving through a tree beside a house; a nest box hung at about ten feet, and most songs were sung at approximately this height.

On my next visit, at 5 PM on 12 May, only typical House Wren songs were heard for several minutes. Then came five combinations, each consisting of a series of three or four Carolina phrases like those heard on 10 May, each series succeeded without pause by a normal House Wren song. It will be noted that many full Carolina Wren songs contain only three or four phrases (Borror, 1956. *Auk*, 73:211–229). Indeed, as I listened to the singer I could also hear the songs of House and Carolina Wrens from several points nearby, and I could detect no differences between these "pure" performances and their respective counterparts in the double vocalizations described. I heard no more combination songs at this time or later, although I passed the yard often during the summer. The wren house in the tree seemed never to be occupied.

A possible connection between the extraneous Carolina notes and a characteristic element of some House Wren songs is suggested by the observations of Kendeigh on the latter bird (1941. *Ill. Biol. Monog.*, 18(3):20). "The song often begins with churring, guttural or sharp staccato notes or squeaks differing from the main body," and the same sounds are sometimes appended as a sort of suffix. While the Carolina phrases described herein may thus be an elaboration of a usually formless part sometimes added to the typical song, this explanation does not account for their imitative effect.

Vocal mimicry in the Troglodytidae is summed up by Armstrong (1955. The Wren, p. 84) with the statement that "as a group [wrens] seem little prone to add to their repertoire by imitation." Saunders (1929. *N.Y. State Mus. Handbook*, 7:31–32) tells of a House Wren lacking all normal song, but although several of its performances suggested those of other species, none did so "clearly enough as to make me think them imitations." In contrast, both the Carolina Wren (Bent, 1948. *U.S. Natl. Mus. Bull.*, 195:211–213; McAtee, 1950. *Wilson Bull.*, 62:136) and Bewick's Wren (*Thryomanes bewickii*) (Howell and Oldys, 1907. *Auk*, 24:149–153) have been regarded as good mimics.

A striking parallel with the present case is Thomas' (1943. *Wilson Bull.*, 55:192–193) report of a wren singing Bewick's and House songs in brief alternate series. This bird appeared to be a typical Bewick's except that its tail may have been shorter than average and was flirted less freely, and Thomas presents the possibility that the singer was a hybrid rather than a Bewick's Wren with an acquired second song. In this connection it

is interesting that both the wrens heard by Thomas and by me were rendering faithful reproductions of the songs of closely related forms, and it may be relevant too to note that Armstrong (*op. cit.*) believes that the Winter Wren (*Troglodytes troglodytes*) does not learn its song but can perform it without having heard others of its species. On the other hand, probably the best argument for caution in explaining a bivalent repertory by assuming hybridization is presented by Lanyon's study of sympatric Eastern and Western Meadowlarks (*Sturnella magna* and *S. neglecta*) (1957. *Publ. Nuttall Orn. Club*, 1:1–67). Although there have been a number of cases of individual meadowlarks with both Eastern and Western songs, Lanyon found that males learn their songs and sometimes those of the other species, and he concluded that there is no clear instance of hybridization in the wild.—Val Nolan, Jr., *Indiana University, Bloomington, Indiana, 4 December 1959.*

House Wrens and Bewick's Wrens in Northern Ohio.—In the spring and summer of 1957 I observed the nesting of a pair of Bewick's Wrens (*Thryomanes bewickii*) in Pepper Pike Village (Cleveland), Cuyahoga County, Ohio. This in itself was a rare and noteworthy occurrence, but even more noteworthy was the fact that the Bewick's Wrens occupied a nesting territory directly adjoining the nesting territory of a pair of House Wrens (*Troglodytes aëdon*).

Sutton (1930. *Wilson Bull.*, 42:13), writing of the nesting wrens of Brooke County, West Virginia, concludes that "the House Wren and Carolina Wren may inhabit precisely the same region without friction; but the House Wren and Bewick's Wren, or the Bewick's Wren and Carolina Wren, evidently do not." Referring to the Bewick's Wren and the House Wren in the vicinity of Johnson City, Tennessee, Tyler and Lyle (1947. *The Migrant*, 18:28–29) state that "when these two wrens meet, they fight to the death." Pough (1946. Audubon Bird Guide, Eastern Land Birds, p. 100) asserts that, "In parts of the Midwest this species [Bewick's Wren] appears to be extending its range northward at the expense of the house wren. Neither will tolerate the other on its breeding territory."

On the afternoon of 21 April 1957, I discovered the male Bewick's Wren in a scrub field area in Pepper Pike Village and observed it for several hours during which time it sang repeatedly. At first it seemed to be wandering about over the field, stopping to sing in the few scattered trees, but later in the afternoon it kept to a small, abandoned orchard at one side of the field. I did not return to the area until 4 May, when I found a pair of Bewick's Wrens in the orchard. They were there on 5 May as well, but on neither day did I hear the male singing.

On the evening of 6 May, I again visited the orchard, finding both Bewick's Wrens there. At about 7:30 PM, for the first time I heard a House Wren in the orchard. Shortly thereafter the male Bewick's Wren and the House Wren began to fight—chasing each other in short flights through the tangled branches of several fallen apple trees in the center of the orchard or occasionally ascending into the crowns of standing trees. Then for some three to four minutes the disputants separated, the House Wren all the while keeping up a vehement scolding. Following this interlude the two birds resumed their fighting which quickly reached its peak of intensity. The scene of this encounter was the dense leafy crown of a fallen apple tree; thus my view of the birds was largely obscured. Occasionally, however, I caught glimpses of them when they flew down among the tussocks of grass beneath the tree, and it seemed that they were actually in physical contact at those times. Throughout the fighting, which lasted for 10 to 12 minutes with only momentary pauses, both birds kept up a furious outcry. One of them (which one I could not determine) uttered a strange squealing note. At the conclusion of these separate encounters, or sometimes just before the close, the Bewick's Wren would often break into song but would

utter only the four opening notes. Throughout the period of fighting, the female Bewick's Wren was nearby and called *plit* repeatedly. When the dispute finally ended, the male Bewick's Wren flew to the topmost branch of a large apple tree in the middle of the orchard and sang his full Song Sparrow-like song as well as a briefer song consisting of first a subdued buzz and then several sweet, clear notes.

Both the Bewick's Wrens and a pair of House Wrens were in the orchard on the morning of 8 May, but they did not engage in fighting. The House Wrens kept to the west end of the orchard, where the male, which sang frequently throughout the morning, was busily cleaning out a cavity in a dead stub of a pear tree. The Bewick's Wrens confined their activities to the eastern half of the orchard.

From 8 May through 15 June, I visited the orchard eight times and spent a total of 17½ hours there. At no time did I observe any conflict between the two species of wrens, nor did I ever see either species go beyond what was approximately the mid-line of the orchard. Located at this mid-line was the large apple tree from which the Bewick's Wren sang at the conclusion of the fight on the evening of 6 May, and from which it sang frequently thereafter. Just once, on the afternoon of 10 May, I observed both the Bewick's Wrens and the male House Wren simultaneously in the central portion of the orchard; the latter was singing. At all other times the House Wrens held to the western half, the Bewick's Wrens to the eastern half, though both species often foraged outside the orchard itself but in areas adjacent to their respective halves. Of the two territories, that of the Bewick's Wrens was considerably the larger. These birds sometimes flew about 200 feet north of the orchard to feed among a brush-grown pile of rocks and rubble, whereas the House Wrens did not go more than 80 or 90 feet beyond the orchard.

On the morning of 9 June, I discovered the nesting site of the Bewick's Wrens in a woodpecker's hole in the dead branch of a fallen apple tree. The branch was parallel to the ground, with the entrance hole on the underside. Both male and female were carrying food to the young. Meanwhile, the House Wrens were nesting in the cavity in the pear tree at the west end of the orchard. The orchard measured 217 feet long and 195 feet wide, and the nest sites of the two wrens were 125 feet apart. The nest site of the Bewick's Wrens was 82 feet in from the east end of the orchard; the site of the House Wren's nest was about 10 feet in from the west end.

When I visited the orchard again on 15 June, the Bewick's Wrens were feeding their five bob-tailed fledglings assembled in the leafy crown of a large fallen apple tree. The House Wrens were still carrying food to their young in the nest in the pear tree. On my final visit on 7 July, the two adult House Wrens and one or two young birds were foraging through the west end of the orchard. In a large hawthorn tree about 100 feet beyond the northwest end of the orchard, two Bewick's Wrens fidgeted about and buzzed frequently.

In the spring and early summer of 1958 I visited the orchard several times but never observed either species of wren there nor anywhere in the immediate vicinity.

According to Williams (1950. Birds of the Cleveland Region, p. 104, 106), the House Wren is a "common migrant; common summer resident" in the vicinity of Cleveland, Ohio, but the Bewick's Wren is a "rare migrant; rare summer resident." Williams cites just one nesting record for the Bewick's Wren: in 1944 at Kent, which is on the southeastern periphery of the Cleveland region. A more recent nesting occurred in the summer of 1952 near Mogadore Lake, which is also at the extreme southeastern boundary of the Cleveland region (Wiley, 1952. *Cleveland Bird Calendar*, 48,3:3). Also, and concurrent with the 1957 nesting of the Bewick's Wrens in Pepper Pike Village, a pair nested successfully in Cuyahoga Falls, Summit County, which is about 25 miles south of Cleveland (Wiley, 1957.

Cleveland Bird Calendar, 53,3:13). The nesting in Pepper Pike Village is the first authentic record for Cuyahoga County.

Elsewhere in northern Ohio the Bewick's Wren is considered rare. Thus to the east of Cleveland, in Ashtabula County, Hicks (1933. *Wilson Bull.*, 45:187) described this species as "very rare and not definitely known to breed." To the west (Toledo), Campbell (1940. *Birds of Lucas County*) described it as "the rarest of the wrens which visit Lucas County." Even in the central portion of Ohio, in the vicinity of Columbus, the Bewick's Wren is classed as an uncommon summer resident (Borror, 1950. A Check List of the Birds of Ohio).—Donald L. Newman, *14174 Superior Road, Cleveland Heights 18, Ohio, 15 February 1960.*

An albinistic Carolina Wren.—Gross (*In* Bent, 1948. *U.S. Natl. Mus. Bull.*, 195:127) reports albinism apparently rare in the Troglodytidae. Since then Bond (1949. *Cassinia*, No. 37:23) has recorded a completely albinistic House Wren (*Troglodytes aëdon*). On 6 December 1959, I banded a Carolina Wren (*Thryothorus ludovicianus*) which when at rest showed a white stripe near the outer edge of each wing, and a touch of white on each side of the lower back. I found that primaries Nos. 5 and 6 in each wing were white to within about half an inch of their tips, where they began shading into normal color, and that one secondary covert in each wing was white to within a short distance of the tip. —Hervey Brackbill, *2620 Poplar Drive, Baltimore 7, Maryland, 9 December 1959.*

Neonates and incubation period of Chimney Swift.—An egg of the Chimney Swift (*Chaetura pelagica*), determined to be fresh by candling on 14 June 1958, was hatched in a forced-draft incubator on 30 June. The pink-skinned neonate hatched 372±11 hours after initiation of artificial incubation. In two other eggs of this clutch that failed to hatch, embryonic development was indiscernible on the sixteenth day. Robert E. Stewart of Laurel, Maryland, donated this clutch from his chimney and Aelred Geis donated another day-old specimen from that locality that was hatched in nature for corroboration.

The incubation period in the artificial incubator of 372±11 hours (15.50±.46 days) contrasts with the incubation period in nature in this species. Whereas MacNamara (1918. *Ottawa Nat.*, 32:39–42) noted a period of 16 days, the period is obviously lengthened considerably by adverse environmental conditions: 19 days has been noted most frequently (Amadon, 1936. *Auk*, 53:216–217; Kendeigh, 1952. *Illinois Biol. Monographs*, 22:1–356; and Sherman, 1952. Birds of an Iowa Dooryard). In the Common Swift (*Apus apus*), the Lacks (1951. *Ibis*, 93:501–546) have shown that the period varies between 18.5 and 24.5 days. The secondary effects of moisture loss from the eggs in depressing egg temperatures may be an important cause of variability, for chimneys are notoriously drafty nesting sites. The methods and conditions of incubation in this study were as previously standardized (Wetherbee, 1959. Artificial incubation of wild birds' eggs and developmental condition of neonates, University Microfilms). The swiftlet looked much like a neonatal passerine except that the toenails, which were duskily pigmented, were extraordinarily long and gracefully pointed, not short and hooked. This character of the toenails was noted previously in another apodiform, the Ruby-throated Hummingbird (*Archilochus colubris*) (Wetherbee, *loc. cit.*). There was also a blunt alular spur, not pigmented, on the swift at hatching. The long toenails are undoubtedly of adaptive significance in clinging to the precariously situated shelf-like nest and also in actual locomotion (see Kennard, *in* Bent, 1940. *U.S. Nat. Mus. Bull.*, 176:275).

The neonates had no down. Four nestlings in the pin-feather stage I took at Gainesville, Florida, also have no signs of natal down. Other workers have noted the absence of natal

down; but it is necessary to corroborate such statements because of the unfortunate lack of objectivity in the literature regarding this point. The generalization that "swifts and hummingbirds are completely naked" at hatching (Wallace, 1955. An Introduction to Ornithology, p. 47), moreover is erroneous, for at least some hummingbird species do have neossoptiles. Downy pterylosis of the Ruby-throated Hummingbird was recently described (Wetherbee, 1958. *Bird-Banding*, 29:232–236). *Apus apus* is hatched naked (Witherby *et al.*, 1938. Handbook of British Birds, 2:248). While Legg (*Condor*, 1956. 58:183–187) described the just-hatched Black Swift (*Cypseloides niger*) as naked, his statement that the two-week-old nestling is completely covered with "down" seems incompatible with his description of the day-old bird unless it is deemed necessary to reopen the argument that neossoptiles might be generated after hatching. Dixon (*Condor*, 1935. 37:265–267) also noted the Black Swift as naked at hatching. Legg (personal communication, 7 October 1955) thought that the "down" might be an adaptation for the nesting habitat of cool and moist situations. It seems probable that what is being referred to here is *not* natal down, but emerging teleoptiles.

There is a very crude correlation between cavity-nesting and nakedness of neonates in passerines (Wetherbee, 1957. *Bull. American Mus. Nat. Hist.*, 113:339–436) that may be applicable in this species. The bill had a dusky pigmentation like that of the toenails and this contrasted with the light pink of the rest of the body. The bill was without special rictal flanges and without special mouth coloration. Therefore, the assumption that the possession of flanges and mouth colors is a specialization for parental guidance in feeding the young in dark nesting cavities (Ticehurst, 1908. *British Birds*, 2:186–194) is not supported, for Barton (*Auk*, 1958. 75:216–217) has demonstrated that this species has had ample time to develop cavity-nesting evolutionary responses.

The eyelids of the neonatal Chimney Swift are closed craniad over the irides at a relatively low level of embryonic differentiation. Fischer (1958. *New York State Museum and Science Service Bull.*, 368) notes that they do not open until the sixteenth to twentieth day after hatching. Considering the disparity in development of the eyes and the feet, we have here an obvious differential acceleration that even defies axial-gradient growth. It is another example of the inadequacy and absurdity of the words "precocial" and "altricial" in ornithology (see Wetherbee, 1959. Comparative phylembryogenetic dimensionality of neonatal birds, University Microfilms).—David Kenneth Wetherbee, *U.S. Fish & Wildlife Service, Massachusetts Cooperative Wildlife Research Unit, University of Massachusetts, Amherst, Massachusetts, 30 November 1959.*

Unusual nesting behavior of Chimney Swifts.—The Chimney Swifts composing a nesting colony on the campus of Kent State University usually pair soon after their annual return in the third week of April. Occasionally a few shift about from one possible mate to another over a brief time, but soon settle down with a mate for that season. However, one female, banded with No. 21-128574, was involved in an unusual type of nesting behavior for this species in the summer of 1959. Her life history is briefly reviewed here.

No. —74 was banded 20 August 1953 as a juvenile bird. She was captured in a flock of 18 swifts composed of both adult and juvenile birds which were roosting together following the nesting period for that season. In 1954, this female returned to the campus, but did not nest. Chimney Swifts do not ordinarily nest until their second year. In 1955, she nested for the first time, in Air Shaft L1. In 1956, she was not recaptured, but the following year she was found nesting in Shaft V1 on the roof of another building. Because this shaft had not been trapped the previous year, it is possible this female had nested there in 1956 as well. When she was found again in 1957, she and her mate had a seasonal

visitor, forming a threesome in Shaft V1. The nature of such nesting by threesomes has already been published by me (1952. *Wilson Bull.*, 64:133–139).

The following year she continued to nest in the same shaft with her same mate, but without a seasonal visitor. In 1959, her mate again returned to Shaft V1 for nesting, but No. ---74 went to Shaft M7 where she roosted for three nights with another female. Seldom are two females found roosting together. The other female soon left and No. ---74 roosted there alone until 16 May. The other female then returned to this shaft with a mate, and they remained there to nest. In the meantime, No. ---74 went into Shaft L1 where she roosted alone until 24 May when she was found in Shaft J1, roosting side by side with another swift. On some nights she was found roosting alone, while other nights she was not located at all. On 7 June, No. ---74 was found working on a nest foundation 13.7 feet down on the west wall. Unlike most nests of the Chimney Swift, this one was not glued to a vertical wall but was placed on a narrow horizontal shelf which projected for a few inches from the wall. On 10 June, an egg was laid, and that evening the female was on the nest while her mate roosted below the nest. On 20 June, the female was found at nighttime roosting alone in an adjacent shaft, J2, while her mate was in J1 roosting beside another female (24-167709), which was captured at that time as a return for the year. This female had been banded the previous August. The nest with the egg prepared by No. ---74 was abandoned. This was the first time that such behavior has been noted among nesting Chimney Swifts. The following night female No. ---09 roosted alone in J1; the other two birds in this threesome were not located. The next day all three dropped out of sight. On 24 June, the male and the replacement female roosted in Shaft J1, about one inch apart, but again ignored the nest with the egg. Two nights later the new female was there alone, but following this date she abandoned this shaft. On 2 July, the original female (No. ---74) returned to J1 where she roosted alone for that night. That same night the other female roosted alone in Shaft L1. In the evening of 16 July, female No. ---09 was again alone in Shaft L1. Four nights later she was there again by herself while the male and his original mate returned to J1, but continued to ignore the nest with its egg. Nesting was never completed by any of these birds that season.

Another instance of unusual behavior is described as follows. The swifts which nested in Shaft N9 in 1958 returned to it in 1959 where they were reunited, but soon dropped out of sight and were not found together again that season until 9 October. On that date they were in a roosting flock of 15 swifts in Shaft V1, but their whereabouts during the nesting season is not known. On 3 June, the male was recaptured for the second and last time in Shaft N9 where he was roosting with three unbanded birds. Two of the newly banded birds (24-167740 and 24-167741) remained in this shaft presumably to nest. However, these birds apparently were incompatible as shown by the following behavior. In the evening of 5 June, No. ---40 was in the shaft alone. Three and four nights later both were present, but roosted six inches apart. In the evening of 10 June, one roosted on the north wall while the other was on the south wall. By this time all of the other resident swifts had completed their nests and most of them were incubating eggs. On 20 June, the two birds were found side by side on the south wall, but the next night they roosted two inches apart. On 22 June, only one roosted for the night in the shaft. Two nights later both were together again roosting five inches apart. On 26 June, one was on the north wall while the other was on the east wall, but the next night they were again side by side on the south wall. On 2 July, they were found roosting on a nest foundation. Progress on nest construction was slow, and on 9 July the birds were found roosting on opposite walls. The nest foundation, 20 feet down on the south wall, was deserted. In the evening of 20 and 21 July, the two birds again roosted side by side on the wall opposite the

deserted nest foundation. On 23 July, they were once more separated, one on the north wall and one on the east wall. Nesting was never completed by these two birds. A similar case of incompatibility was reported earlier by me (1951. *Amer. Midl. Nat.*, 46: 227–229).—RALPH W. DEXTER, *Department of Biology, Kent State University, Kent, Ohio, 10 March 1960.*

Downy Woodpeckers scaling bark on diseased elms.—Woodpecker activities may, at certain times, have interesting associations with diseases of trees. West and Spiers (1959. *Wilson Bull.*, 71: 348–363) mentioned that some of the three-toed woodpeckers which invaded southward in 1956–1957 were observed chipping off the outer bark of elms, thus revealing the fawn-colored inner bark. One observer suggested that the invaders were seeking the *Scolytus* beetle, which is a vector of the Dutch elm disease. This disease is important in the ecology of woodpeckers in the vicinity of Seneca, Maryland, for I have found the nest holes of Pileated (*Dryocopus pileatus*), Red-bellied (*Centurus carolinus*), and Downy and Hairy Woodpeckers (*Dendrocopus pubescens* and *D. villosus*) in trees killed by its effects. Diseased elms are recognizable by the engraving of multibranching tunnels which the beetle provides for its eggs and larvae. Of the above species, only those of the genus *Dendrocopus* consistently feed on the various stages of *Scolytus*, which occur in great concentration in the bark of some elms. This food supply attracts Downy Woodpeckers in particular. In observations made from 1956 to 1959, I have noticed that these woodpeckers may begin scaling the bark on dying elms as early as 15 September, and continue to do so until late in April. I have seen as many as four of them busy on one elm. Flakes of bark litter the ground below such trees, and trunks and limbs become fawn-colored as the openings of hundreds of minute tunnels are revealed. Such elms are of no further interest to the woodpeckers in a succeeding year. The remaining bark begins to fall off in large pieces at this time. Hairy Woodpeckers work on diseased elms in much the same manner, but I have only a few records of their doing so. The report of West and Spiers that *Picoides articus* and *P. tridactylus* both fed on elms during their invasion is of interest, among other reasons, because the bark-scaling activity appears to be especially characteristic of the genus *Dendrocopus* and systematists regard *Picoides* and *Dendrocopus* as belonging to closely related genera.—LAWRENCE KILHAM, *7815 Aberdeen Road, Bethesda 14, Maryland, 21 January 1960.*

A winter record of the Forster's Tern for Rhode Island.—On 6 January 1960, an immature Forster's Tern (*Sterna forsteri*) was seen along the shores of the Sakonnet River in Middletown, Newport County, Rhode Island. When first seen the bird was perched on a buoy about 400 feet from shore; it later flew along the shoreline and passed within 50 feet of my car. While on the buoy, it was studied for several minutes through a 20× telescope and it was especially noted that the dark patch behind the eye was restricted and did not extend around the nape. Later, when the bird was seen in flight, the paleness of the upper parts was particularly conspicuous. A half-hour after the original sighting I returned to collect the bird but it had disappeared. It should be noted, therefore, that (1) the bird was observed for 10 or more minutes under the best of conditions (at noon on a bright clear day), (2) it is a species well-known to me, and (3) I was fully aware at the time of the unique aspect of the record. A check of the literature indicates that this is the first winter record of this species for Rhode Island, and the latest winter record north of Cape May, New Jersey.—JAMES BAIRD, *Norman Bird Sanctuary, Third Beach Road, Middletown, Rhode Island, 29 January 1960.*

LETTER TO THE EDITOR

In *The Wilson Bulletin* for September 1958 (p. 281), appears an account of the Spotted Sandpiper escaping a Cooper's Hawk by diving into the water. The authors, Martin and Atkeson, say they have not found another instance in the literature. However, in *The Auk* of July 1928 (p. 371), I recorded a similar incident, which occurred long ago, a boyhood observation on the Red River in Minnesota. It must have been about 1906, and I can only determine that it was either a Sharp-shinned or a Cooper's Hawk.

On 4 September 1914, on Charlton Island in southern James Bay, Canada, while approaching a turnstone on the beach, I heard a "swish" close by and saw a small hawk, which looked like a Pigeon Hawk, slanting down to the water's edge after a Spotted Sandpiper. The sandpiper flew out over the water, could not dodge, so dropped into the water and went below the surface. The hawk flew on.

These incidents in Minnesota, Alabama, and Canada show that the Spotted Sandpiper, wherever it may be, does not hesitate to go into water, and there can handle itself very well.—OLAUS J. MURIE, *Moose, Wyoming, 8 January 1960.*

NEW LIFE MEMBER

The photograph shows Walter R. Spofford, new life member of the Society, photographing a nest of Golden Eagles in the Appalachian Mountains last June. An Associate Professor of Neuroanatomy at the State University New York Medical College, and a graduate (Ph.D.) of Yale University, Mr. Spofford is presently working on biochemical systematics with egg-white proteins in the Falconiformes. He is also interested in molting patterns, distribution, and life histories of falconiform birds (especially the Appalachian Golden Eagles). His papers and notes are on experimental neuroembryology, molting in *Cyr* Falcons and Golden Eagles, and tree-nesting of Peregrine Falcons. Mr. Spofford has been an active member of the WOS since 1928, is a life member of the AOU, and an active member of the BOU, Cooper Ornithological Society, Linnaean Society of New York, Tennessee Ornithological Society, Federation of New York Bird Clubs, Avicultural Society, and the Falconry Club of America.

ORNITHOLOGICAL NEWS

LOUIS AGASSIZ FUERTES RESEARCH GRANT

This grant, established in 1947, is devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic organizations. Each proposal is considered primarily on the basis of possible contributions to ornithological knowledge.

An anonymous donor gave $500 to found the fund; later donors have provided some $600. The Council of the Wilson Ornithological Society has added funds as necessary to provide at least one $100 grant annually.

Although grantees are not required to publish their studies in *The Wilson Bulletin*, it is hoped that they will submit their manuscripts to the Editor of the *Bulletin* for consideration.

Since its inception the Fuertes Research Grant has been awarded to 15 persons, many of whom have continued their research work. The recipients are listed below.

1948—Leonard R. Mewaldt, Life history of Clark's Nutcracker.
1949—Stephen W. Eaton, A comparative study of the genus *Seiurus*.
1950—Henry E. Childs, Population dynamics and life history of the Brown Towhee.
Byron E. Harrell, Ecology of the Rancho del Cielo, Tamaulipas, Mexico.
Arnold J. Petersen, Reproductive cycle in the Bank Swallow.
Harrison B. Tordoff, Comparative osteology of the subfamilies of the Fringillidae.
1951—Howard L. Cogswell, Territory size and its relation to vegetation structure and density among birds of the chaparral.
1952—Robert W. Nero, Territorial and sexual behavior in the Red-wing.
1953—No award.
1954—William C. Dilger, The isolating mechanisms and relationships of the thrush genus *Hylocichla*.
1955—Robert G. Wolk, Analysis of reproductive behavior in the Black Skimmer.
1956—John B. Millar, An investigation of possible factors involved in the initiation of migration.
Lester L. Short, Jr., Hybridization and isolating mechanisms in North American flickers.
1957—Millicent (Mrs. Robert L.) Ficken, Comparative study of the behavior of the Canada Warbler and the Redstart.
1958—Harold D. Mahan, Studies of growth and temperature regulation in the Red-wing.
1959—No award.
1960—Robert T. Lynn, Comparative behavior of the Carolina and Bewick's Wrens.

Application forms may be obtained from Harvey I. Fisher, Southern Illinois University, Carbondale, Illinois. Completed applications must be received by 15 April 1961.

On 9 January, the New York Zoological Society awarded its gold medal to Dr. Roger Tory Peterson as "an inspired interpreter of birds for the benefit of mankind."

The first triennial award of the Gill Memorial Medal of the South African Ornithological Society for contributions to ornithology south of the Zambezi has been made to Dr. J. M. Winterbottom, Hon. Secretary of the Society since 1951 and Director of the Percy Fitzpatrick Institute of African Ornithology.

FROM THE AOU

The Josselyn Van Tyne Memorial Fund will have a sum of $300 available for research awards at the end of the fiscal year, 31 July 1961. Any student of birds is invited to apply for part or all of this amount.

Ten duplicate copies of an application are desired for distribution to members of the Research Committee who will determine how the funds will be allotted. The application should give a full description of the proposed research, the type of help required (equipment, travel, assistance, etc.), the amount of money desired, and the background and training of the applicant. With young men or women just starting their careers, a supporting letter from one or more recognized ornithologist would be helpful.

Applications should be submitted not later than 1 June 1961, to S. C. Kendeigh, Chairman, Vivarium Building, University of Illinois, Wright and Healey Sts., Champaign, Illinois.

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the Life Sciences is 15 May 1961. Proposals received prior to that date will be reviewed at the summer meetings of the Foundation's advisory panels and disposition will be made approximately four months following the closing date. Proposals received after the 15 May 1961 closing date will be reviewed following the fall closing date of 15 September 1961.

Inquiries should be addressed to the Biological and Medical Science Division, National Science Foundation, Washington 25, D.C.

REQUESTS FOR INFORMATION

Alarmed by persistent reports of a downward trend in the population of Bald Eagles, the National Audubon Society has launched a study aimed at determining the status of the species. This project is designed to cover at least five years and to gather data from all parts of North America. The study will consist of two parts, first an inventory based on the number of active nests located, and second an investigation of various aspects of eagle biology. Information is urgently needed on the location of active eagle nests and also on wintering concentrations of eagles. If you have information on these or any other facets of eagle biology, please communicate with: Alexander Sprunt IV, Box 231, Tavernier, Florida.

I have been studying the life history of the Pigeon Hawk (*Falco columbarius richardsonii*) in western Saskatchewan and I would appreciate any information on the following topics from other parts of this species' range: migration dates, nesting dates, nesting habitat, location and type of nest, clutch size, brood size, sex ratio of young, food habits, species hawks defend territory against, unusual behavior of any kind, habits of wintering birds, habitat during winter, and interspecific agonistic relationships. I would also appreciate any data on sex and weight of specimens in private collections. Please send all information to Glen A. Fox, Box 783, Kindersley, Saskatchewan, Canada.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

Books: List B-5

The following titles are of books added to the library since publication of List B-4, in December 1958 (*Wilson Bulletin*, 70: 384–385).

Those wishing reprints of this and the earlier book lists should contact the Josselyn Van Tyne Memorial Library (Wilson Ornithological Society), Museum of Zoology, The University of Michigan, Ann Arbor, Michigan.

Agassiz, L., H. E. Strickland, and W. Jardine, Bibliographia Zoologiae et Geologiae. 4 vols. 1848–54.

Bailey, A. M., Birds of Arctic Alaska. 1948.

Ball, S. C., Fall Bird Migration on the Gaspé Peninsula. 1952.

Bannerman, D. A., Birds of the British Isles. Vol 5. 1956.

——— and W. Mary, Birds of Cyprus. 1958.

Behle, W. H., The Bird Life of Great Salt Lake. 1959.

British Museum, Catalogue of the Books, Manuscripts, Maps and Drawings in the British Museum (Natural History). 7 vols. 1903–33.

Brown, L., Eagles. 1955.

Capen, E. A., Oölogy of New England. 1886.

Carus, J. V., and W. Engelmann, Bibliotheca Historico-Naturalis, 1846–60. 2 vols. 1861.

Congdon, R. T., Our Beautiful Western Birds. 1954.

Curry-Lindahl, Kai, Nagra Svenska Faglar. 1947.

Dixon, J. S., Birds and Mammals of Mount McKinley National Park. 1938.

Engelmann, W., Bibliotheca Historico-Naturalis, 1700–1846. 1846.

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* * *

The following gifts have been recently received. From:

Andrew J. Berger—1 reprint
W. H. Burt—2 pamphlets, 7 reprints
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NEW LIFE MEMBER

M. Albert Linton, of Moorestown, New Jersey, an active member since 1941, has recently become a life member of the Society. Mr. Linton holds B.S. and M.A. degrees from Haverford College, did graduate work at Switzerland's Federal Polytechnic Institute in Zürich, and received an honorary LL.D. from Ohio's Miami University. A former President (20 years) and Chairman of the Board of Directors (5 years) of the Provident Mutual Life Insurance Company of Philadelphia, Mr. Linton has somehow found time to be an "amateur bird watcher for over 50 years," President of the Philadelphia Academy of Sciences, a Fellow of the Delaware Valley Ornithological Club, and a member of the AOU and the Cooper Ornithological Society.

THE STATUS OF WATERFOWL CONSERVATION

A Contribution from the Wilson Ornithological Society Conservation Committee

The effort to protect waterfowl from excessive hunting and to preserve essential habitat to meet seasonal needs has been moving at an ever-increasing tempo. Recently, attention has been directed toward providing space on which the public may enjoy waterfowl hunting and observation. The objective of this report is an appraisal of accomplishments.

ACKNOWLEDGMENTS

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HABITAT MANAGEMENT

Behavioral characteristics of waterfowl dictate that acceptable habitat must be available for breeding, migration, and wintering. Deficiencies in any of the three functional types of habitat, but especially breeding and wintering areas, can depress populations and/or create more complex management problems. However, recognizing that sizable investments have already been made in migration and wintering habitat, the greatest need for habitat expansion now is believed to center on the breeding grounds. Unless a sufficient volume of birds is produced, present and future demands of hunters and nonhunters will not be met, and populations on migration and wintering areas will be disappointing.

Breeding Habitat.—Not all aquatic habitat provides the essential features to satisfy the needs and preferences of waterfowl during the breeding season. The region most productive of ducks and coots is the "Prairie Pothole Region." It extends over an area of 217,000 square miles in south central Canada and the northern Great Plains in the United States (U.S. Fish and Wildlife Service, 1953:3). Included in it are 161,000 square miles in Canada (Alberta, Saskatchewan, and Manitoba) and 56,000 square miles in the United States (North Dakota, South Dakota, and Minnesota).

Specific figures on the number and acreage of wetlands important for breeding waterfowl are unavailable for the entire pothole region. In Canada, wetland inventories are in initial planning or operational stages. Estimates for the U.S. portion in the mid-1950's showed 1,210,000 wetland depressions totaling 4,450,000 acres. Within the 91 key counties in the tri-state area of North Dakota, South Dakota, and Minnesota, an estimated 2,820,000 acres of prime duck and coot production habitat were present. This 91-county area contains the last extensive, top-quality, natural breeding habitat in the United States.

The importance of this pothole area is indicated by waterfowl population figures obtained between 1950–57. Approximately one-half (53 per cent) of the continental duck supply was produced in the North American Prairie Pothole Region (Hawkins *et al.*, 1958). The U.S. portion of this region contributed about 14 per cent of the total production.

Nonpothole type of breeding habitat exists as separate segments in an area upwards of one and one-half million square miles, largely in Canada. These remote and comparatively stable aquatic areas accommodated slightly under 47 per cent of the total breeding duck population in the 1950's. In addition to producing over 80 per cent of the continent's duck supply, Canada also produces the bulk of the coots and geese.

Demands for waterfowl already exceed existing populations. Thus, management's task is to maintain the existing volume of flights and to increase them where possible. In North America, maintenance of the numerous, small, shallow depressions accommodating breeding ducks and coots constitutes the most challenging issue faced by waterfowl managers. The potholes exist in a matrix of soils developed for an agricultural economy. In cropland areas these small wetlands impede tillage with modern machinery and are considered a nuisance. Consequently, land-owners are converting the bothersome wet areas to cropland by draining and filling. This destruction is in an initial stage in Canada. In the United States it is in a final stage. The ducks are caught in a familiar squeeze where the actions of individuals eliminate public resources or values as they develop land to maximize economic returns. Unfortunately, individual choices in land developments usually do not recognize public or national values.

A controversial issue in the United States resolves itself around the fact that technical assistance and cost-sharing are provided by the government to accomplish drainage. The rate of loss of these extremely valuable duck and coot producing areas is accelerated by these incentives.

To date, losses of potholes have exceeded preservation efforts. The magnitude of subtractions are indicated by the following examples. Historically, the prairie pothole area in the U.S. covered 115,000 square miles. Man, largely through drainage, has practically removed all potholes in slightly more than one-half of the area (an estimated 56,000 square miles remained in the early 1950's). Within the remaining portion, federally assisted drainage—not counting locally financed projects—claimed 256,700 acres of prairie duck habitat between 1951 and 1955 (Reuss, 1958:3). During the same period, a total of 3,462 acres of all types of habitat was acquired for waterfowl in the three prairie pothole states by the U.S. Fish and Wildlife Service. In other words, the federal Agricultural Conservation Program removed a little more than 74 times as many acres of wetlands as were acquired by the Federal Government for waterfowl purposes. Farm drainage is continuing. In North Dakota, South Dakota, and Minnesota, drainage increased sharply in 1958 over the average of the three preceding years (Seaton, 1959:391). An estimated 10,000 potholes were drained in this single year. Under existing governmental guidelines, Morgan (1960:8) estimates that eventually 90 per cent of the wet areas of the region will be lost through federally subsidized drainage.

How many years it will take to destroy the remaining breeding habitat is unknown. However, one thing is certain. The technology and horsepower are available to accomplish the task. Drainage and land leveling are now perfected land improvement techniques. Modern machinery has provided landowners with additional time and the means to convert their wet depressions to cropland. For example, one farmer using a three-bottom, 16-inch tractor plow cutting 48 inches and traveling at 3¼ miles per hour, can plow approximately 13 acres in 8 hours of running time. This is about five times the acreage plowed in a day in the 1920's by one man using three horses.

In Canada, both draining and filling of duck breeding habitat, although still in early stages of development, are growing in importance (Hawkins and Jahn, 1960; Moulding, 1960; L. B. Keith, pers. comm., 1960). In certain provinces, governmental assistance is provided for draining and clearing land for crop production (Hopkins, 1952:212).

Various approaches continue to be used to preserve essential duck and coot breeding sites. Some suitable habitat is provided indirectly as small water areas are established, largely to provide livestock with water. In Canada, neither the Canadian Wildlife Service nor the the provincial game branches own any pothole-type habitat. Lack of funds limits their programs. As mentioned previously, some wetland surveys are being planned or have been initiated recently to define more clearly the preservation task.

Two agencies working in Canada have provided duck and coot breeding habitat. Since the Prairie Farm Rehabilitation Act was passed in 1935, the Canadian government has constructed over 56,000 small water areas, primarily to provide water for farm purposes. Secondarily, a small proportion of these areas accommodate breeding ducks. Ducks Unlimited has made some of the most important contributions to the preservation and development of lands for waterfowl. Between initiation of the work in 1938 and 1 March 1960, development has been carried out on 519 projects comprising 788,000 acres of water and having 4,457 miles of shoreline (W. B. Leitch, pers. comm., 1960). Ducks Unlimited owns no land. All projects are established by securing flood easements from landowners.

In the United States, individual landowners carry out practices that add as well as subtract duck breeding habitat. Additions occur primarily as incidental benefits on lands modified to provide water for livestock and the irrigation of crops. In natural grassland areas used mainly for grazing, livestock ponds, in some cases, provide new homes for breeding ducks. However, annual production of ducks per square mile averages 10 to 15 ducklings in the stock pond region of western North Dakota, South Dakota, and eastern Montana, compared to 100 to 150 in good prairie pothole country (U.S. Fish and Wildlife Service, 1953:7). While these additions of duck breeding habitat are of some value, they neither replace the millions of top quality acres already lost, nor do they compensate entirely for the potholes now being destroyed.

Extensive efforts through legislative, educational, and voluntary avenues of approach have been made in the United States to save the potholes from destruction. Attempts to pass bills in the 86th Congress to halt government technical assistance and cost sharing for farm drainage harmful to wildlife, especially breeding waterfowl, failed to make substantial progress. That congressional action is required to change the policy of the Department of Agriculture is clear. Since 1956, Congress has declared that no conservation practice may be dropped by anyone, except the county committees of the Agricultural Stabilization and Conservation Program. This is truly a grass roots type of program. Since the rate of drainage increased between 1956 and 1958, it is evident that in the pothole region the county committees did not abandon or reduce drainage programs.

Another attempt to maintain potholes was advanced in May of 1960. A Memorandum of Agreement between the Bureau of Sport Fisheries and Wildlife, the Soil Conservation Service, and the Agricultural Conservation Program, provides for cooperation between the three agencies in reviewing wildlife values on lands for which farmers have requested cost sharing for drainage in designated pothole counties in Minnesota, North Dakota, and South Dakota. Established procedures permit wildlife technicians to advise the landowners of wildlife values on the lands, alternatives for management, and the existing government programs of land purchase and lease for wildlife. However, it must be clearly recognized that the county committees have final authority for approval or disapproval of cost sharing on drainage applications.

To save a portion of the potholes, government programs of land acquisition have been expanded in recent years. "Save The Wetlands" committees in the Dakotas and Minnesota have energetically brought the story to the public since the mid-1950's and have helped secure limited donations of money for wetland preservation. In these three states, 221,718

acres of waterfowl habitat were purchased between 1940 and 30 June 1960, under the Pittman-Robertson Federal Aid in Wildlife Restoration Act. A little less than 100,000 acres of this total are prime waterfowl breeding habitat. Insufficient funds continue to hamper the state acquisition programs.

An important step to accelerate the federal acquisition program was initiated in 1958. An amendment to the federal Migratory Bird Hunting Stamp Act raised the price of the Duck Stamp from $2.00 to $3.00, and designated that, beginning 1 July 1960, all of the receipts from the sale of stamps, less the cost of printing and distribution, should be spent to acquire lands for waterfowl. Many states, through their Flyway Councils, are enthusiastically urging the Bureau of Sports Fisheries and Wildlife to spend the bulk of the money for preservation of breeding habitat. To date, three federal waterfowl production habitat acquisition stations have been established in North and South Dakota. This program, in its initial phases, consists of securing good quality, duck-producing units through a combination of purchase and easement. A duck production unit consists of a number of temporary water depressions surrounding a more permanent water area required for rearing broods. Availability of experienced personnel now limits expansion of this approach to habitat preservation. Only time will tell how many production units will be saved from drainage. One thing is certain. It will be a tough race, since the rate of drainage has been increasing.

Certain key waterfowl production centers in the nonpothole type habitat are also being threatened by activities of man. Protection of the breeding grounds of the Blue and Snow Geese on the southwest side of Baffin Island became an urgent matter as a result of keen interest recently shown in the mineral resources of that general region (Munro, 1957:10). This area supports one of the world's most important goose colonies, with about 500,000 birds involved. Interest centered around intensive mineral exploration and exploitation of iron ore through open pit mining. Such activities would seriously disturb the geese. Open pit mining would consume space used by the birds and would convert breeding habitat to unsuitable types. The problem has been successfully met by establishing two types of reserved areas. Within a 500-square-mile area containing the heart of the colony of geese, industrial activities and hunting are strictly prohibited. This area is known as the Bowman Bay Game Sanctuary. Surrounding it is the 3,150-square-mile Dewey Soper Bird Sanctuary which serves as a sort of buffer zone. Hunting is prohibited, prospecting may be allowed under permit from the Canadian Wildlife Service, and mining development may be permitted, providing adequate steps are taken to prevent undue disturbance of the geese.

Thus, we see that man is destroying or threatening to destroy a large part of the most productive waterfowl breeding grounds. From goose breeding concentrations in the northern tundra to the more southerly prairie production centers of ducks and coots, individuals or small groups of people are attempting to convert the prime breeding habitat to other land uses. To protect one of the world's largest breeding colonies of geese, regulations have been adopted which restrict individual action for the purpose of aiding the larger public welfare. In our modern society, such procedures are not new.

Some approach, in addition to governmental acquisition, appears necessary to save a large part of the prairie pothole type duck and coot breeding habitat. Farmers now own and occupy the bulk of the area. Soils in the bottom of many potholes are capable of producing crops. In the United States, much of the cropland matrix in which the potholes exist should be converted to grassland to reduce wind and water erosion and provide a more stable agricultural economy (Kimball, 1953; Clawson, Held, and Stoddard, 1960:460). If converted to grazing land, many of the potholes would furnish water for

livestock as a part of improved range management. How to bring about this conversion is the challenge now facing citizens. One suggestion is to establish a mixed federal-state-private corporation to buy, develop, and manage grazing land (Clawson, 1958). Time provides the base on which to measure the success of the various attempts used to maintain the essential breeding habitat. But we must recognize that time to preserve the potholes is rapidly decreasing.

Migration and Wintering Habitat.—This discussion of migration and wintering habitat centers on the United States, for it is here that the greatest pressures are on the land at this time. There is no immediate need to consider the status of habitat in Canada and south of the United States in detail. Generally, the status of migration habitat is in a healthy condition in Canada. From the United States-Mexico border to northern South America the majority of the wintering areas, despite some local reductions in carrying capacity, can still accommodate more waterfowl than now use them (Hawkins *et al.*, 1958).

In the United States, maintenance and development of migration and wintering areas for waterfowl are carried out by private interests and governmental agencies. The combination of these efforts contribute toward providing suitable habitat to enhance the distribution and survival of waterfowl and to increase or maintain recreational opportunities.

Private Management. Actions of private interests to benefit waterfowl are much larger in scope than is commonly realized. In the Mississippi Flyway, at least 75 per cent of the nearly 10 million acres of waterfowl habitat under some form of management is privately controlled (Hawkins *et al.*, 1958). In the four states of Illinois, Missouri, Arkansas, and Louisiana, clubs control approximately 3,200,000 acres (Hawkins *et al.*, 1960:17). More than 800 duck clubs control 200,000 acres of land in California (Scheffer, 1959:238). Increased numbers of private landowners in the Pacific Flyway are showing interest in developing and managing lands for waterfowl through plans provided by technicians of the Soil Conservation Service.

Experiences of some of these clubs clearly demonstrate that intensive management aimed at providing preferred feeding and resting areas results in high duck-use. For example, a single duck club in Illinois and another in Arkansas have at one time held close to one-fifth of the Mississippi Flyway's Mallard population (Hawkins *et al.*, 1960:18). While such large concentrations of Mallards reduce the possibilities of having the birds widely distributed, they very vividly demonstrate the capabilities of privately managed areas to accommodate ducks.

Throughout the country, the incentive of securing shooting opportunities has resulted in the management of millions of acres of habitat for waterfowl. In addition, between 1935 and 1 July 1959, a total of 994,000 farm ponds had been constructed with government aid (U.S. Soil Conservation Service, 1960). When the hunting season closes, these private areas benefit ducks and geese. As hunting pressure increases in the future, more acreage will probably be developed by private interests. Such efforts will provide recreational opportunities for people and living space for waterfowl.

Government Management. As in the breeding grounds, conflicting land- and water-use programs are affecting waterfowl migration and wintering habitat. Draining, filling, and flooding have been and are taking place on an extensive scale to modify wetlands for agriculture, navigation, power, industry, and real estate. In this process prime aquatic habitat is destroyed. Studies indicate that approximately one-third of the natural wetlands in this country have been lost (Shaw and Fredine, 1956:7). In natural lakes and streams, aquatic foods, although enhanced in some cases, have generally been reduced by pollution, siltation, and chemical treatments to improve boating and swimming facilities. Con-

servation organizations are attempting to offset these losses by acquiring lands and working cooperatively with other agencies, such as the Corps of Engineers and Bureau of Reclamation, to mitigate the harmful effects of water development projects and to improve habitat for wildlife.

Federal and state governments started acquiring habitat for waterfowl in the early 1900's. Their efforts were formalized into a specific goal in 1934. A minimum of 12,500,000 acres of land managed primarily for waterfowl was believed needed. With approximately 3,300,000 acres obtained by 1 January 1957, the U.S. Fish and Wildlife Service still has to acquire a little over 4,000,000 acres to reach its share of the objective, or a total of 7,500,000 acres (Select Committee on National Water Resources, 1960:52). Ultimately the Service hopes to have an important waterfowl refuge every 200 miles along the north-south axis of each of the four flyways.

States, with approximately 1,450,000 acres of land for waterfowl, need to secure an additional 3,550,000 acres to meet their minimum objective of 5,000,000 acres. Obtaining the remaining acreage is becoming a more difficult task. There are fewer willing sellers (Jorgensen, 1957:4). Land prices are increasing, and some local governments oppose removal of more land from the tax rolls.

In addition to these acquisition efforts, much has been accomplished in establishing and improving federal policies and programs designed to replace and develop waterfowl habitat as a part of the nation's military and water resources programs. Legislation enacted in 1958 and 1960 advanced the opportunities for developing migration and wintering areas through inter-agency cooperation. One important new feature is that federal construction agencies now have the authority to incorporate fish and wildlife conservation and enhancement features into project planning, including the acquisition of additional lands to benefit fish and wildlife. Possibilities for developing waterfowl habitat under these new provisions are only starting to be realized. Plans on one project, the Army Corps of Engineers' navigation project on the Tombigbee River in Alabama, call for acquisition of land for the new Choctaw National Wildlife Refuge. This is the first instance where land will be purchased for wildlife at the site of a federal public works project, under the terms of the new 1958 legislation. Similar possibilities seem certain in the future. It is expected that reservoirs will double in area from 10,000,000 acres in 1950 to 20,000,000 acres by 2000 (Clawson, Held, and Stoddard, 1960:442). This expansion program deserves close attention. Potentially, tremendous opportunities exist for benefiting waterfowl and for providing public recreational opportunities.

Another cooperative endeavor that could provide aquatic habitat is the small watershed program which was established in 1954. Through cooperative efforts of the Soil Conservation Service, Forest Service, Fish and Wildlife Service, Soil Conservation Districts, and local watershed associations, features benefiting wildlife can be worked into the over-all watershed plan for proper soil and water management. Federal cost sharing is available for project modifications benefiting wildlife. Potentially, benefits to waterfowl could be considerable. However, local sponsoring groups have used the provisions relating to wildlife very little (Select Committee on National Water Resources, 1960:35). In fact, in Minnesota, anticipated losses of existing wildlife habitat would be great within the boundaries of some watershed proposals (Vesall, 1955:4).

A third cooperative measure, established in 1960, provides for development of suitable environments for fish and wildlife on property controlled by the U.S. Armed Forces. Provisions permit state wildlife agencies and administering officers of bases to provide public hunting and fishing on military reservations, using funds from service fees to improve the areas for these activities. Some habitat will be managed for waterfowl.

For a more detailed account of resources programs affecting waterfowl habitat, see the excellent bulletin issued by a select committee of the United States Senate (Select Committee on National Water Resources, 1960).

In summary, progress, although slower than desired, is being made to maintain and develop migration and wintering habitat in the United States. Private interests are managing significant acreages of top quality habitat. Future opportunities for developing migration and wintering habitat appear good, especially in conjunction with federal public works water development projects and on military lands. Nevertheless, under anticipated future intensive use of land and water, losses in suitable acreage are expected to exceed gains. Hope for accommodating large numbers of waterfowl on lesser acreage rests on the fact that the birds will concentrate on specific areas in spring, fall, and winter. Experience definitely shows that on intensively managed areas, large numbers of waterfowl can be accommodated, although the distribution of the birds is more restricted.

POPULATION MANAGEMENT

Waterfowl population management consists primarily of gearing the annual harvest to the yearly surplus and minimizing losses due to causes other than hunting. Objectives of the program include maintaining a widely distributed population of waterfowl at a sufficiently high level to provide both hunters and nonhunters with recreational opportunities on a sustained basis without causing undue hardships to agricultural and other interests. Investigations and management experiences have contributed substantially toward developing the base of information required to satisfy the goals. Some recent advances involving research, regulations, and depredations-control have been especially noteworthy.

Research.—In recent years investigations have covered broad geographic areas through cooperative undertakings. Generally, Canadian and United States federal wildlife agencies have provided leadership and materials. States and provinces, through their Flyway Councils, have contributed manpower, equipment, and funds. Other private organizations, such as Ducks Unlimited, and certain educational institutions, participated in a manner similar to that of the states. The Wildlife Management Institute, North American Wildlife Foundation, and National Wildlife Federation encouraged the investigations and contributed to them. Through combined efforts of these groups, population appraisals, banding, harvest studies, and depredation surveys have been intensified in Canada and the United States. One of the most significant results has been the development of a system to collect wings from ducks bagged by hunters in the United States. Species composition of the kill, age ratios to check on reproductive success, and other characteristics of the kill have been obtained from the wings. Partnership surveys definitely appear to be the most effective means for securing adequate population information over the broad geographic range covered by waterfowl.

Regulations.—One of the important advances in regulations has involved protection of Canvasbacks and Redheads. These over-water nesters were particularly hard hit by drought on the breeding grounds in the late 1950's. Recovery of the emergent aquatic nesting cover in 1960 was, in many areas of the prime breeding range, excellent. With normal water conditions, it is anticipated that nesting cover will be ideal in the spring of 1961. To provide for rapid recovery of Canvasback and Redhead populations, the U.S. Bureau of Sports Fisheries and Wildlife, with support from the Flyway Councils, closed the season on these two species in 1960 in an attempt to return as many of the birds as possible to the breeding grounds in 1961 (Janzen, 1960:2). Another step, which some people believe should already be employed to prevent waste, is to close the key Redhead and Canvasback concentration sites to all waterfowl hunting. This action would eliminate

the kill which takes place as a result of the hunter's inability to identify species in flight.

Another significant regulation of 1960 which advanced species management involved the Canada Geese of the Mississippi Valley, specifically those that winter primarily in southern Illinois and adjacent areas. This population is well known for the excessive kill it suffered in the mid-1940's. Attempts are now being made to manage it on a state quota basis to provide maximum sustained public recreational opportunities. To insure a large nucleus of breeders and to permit recovery of the declining flock, a kill quota was established in 1960 for certain counties within the two states where a large portion of the annual harvest takes place. Wisconsin's share was set at 7,000 and Illinois' at 14,000. This action recognizes the fact that the size of a flyway or species population depends upon the sum of the birds in each subpopulation or flock. Regulations aimed at maintaining or increasing separate flocks is definitely a forward step toward improving population management. As long as wintering grounds are adequate, limiting hunting mortality on each of the separate flocks appears to be the most effective way to permit Canada Geese to increase and fully utilize their remote and stable breeding grounds. Sportsmen in Wisconsin and Illinois are to be congratulated for accepting the required restrictive regulations with very few complaints.

Depredations Control.—Grain-eating Mallards and Pintails continue to offend Canadian wheat farmers by consuming and trampling large quantities of grain. Crop losses are substantial in some years. In 1955, estimates indicated that losses totaled $10,500,000 in Saskatchewan (Elkins, 1957:1). These depredations constitute a barrier which threatens to block preservation of the highly productive duck and coot breeding grounds in the agricultural parts of Canada (Leitch, 1960:18). Farmers suffering damage generally consider ducks more a pest than anything else. Unfortunately, all species of ducks suffer from adverse attitudes and activities of farmers caused by two upland feeding species, namely the Mallard and Pintail.

Cooperative investigations have been conducted in Canada during the past few years to determine the characteristics of the depredation problem and to test various control measures. The most important control measure tried was the automatic acetylene exploder, which prevented duck depredations on small parcels of land (Stephen, 1959:1). Trials were conducted in September of 1960 to determine whether or not the exploders would also prevent damage on a large block of cropland.

In addition to these tests, other attempts to deal with the problem have been tried. Scaring and herding techniques have been used. Permits have been issued to shoot in unharvested crop fields. In the Province of Saskatchewan, insurance is available to farmers to protect them against crop losses caused by wildlife. In Manitoba, a feeding program was tried, with some success, near the Delta marshes. These methods have helped meet the problem in some areas. However, additional solutions are required to resolve more fully the conflict between grain-feeding ducks and farmers. What is needed is a preventive or compensatory plan that will operate continuously over a broad geographic area, regardless of weather and road conditions.

In the Pacific Flyway, especially California, crop damage by the Mallard, Pintail, American Widgeon, and coot was severe in some localities. The most effective measure in controlling depredations here was the development of strategically located feeding, watering, and resting areas (Lostetter, 1960:102).

FUTURE NEEDS

The major immediate needs to conserve waterfowl are known. Prairie pothole type breeding habitat must be preserved, especially on the Canadian prairie. Crop depreda-

tions must be controlled. Hunting mortality must continue to be regulated in relation to the status of populations, particularly for individual species and manageable flocks.

With the expansion of human population, solutions to these problems will become increasingly more challenging. Greater public understanding and support, adequate financing, and a continuous flow of factual information will be required to permit courageous and imaginative leaders to guide and improve waterfowl management within the anticipated future environmental conditions.

That a large segment of the public does not now recognize the need for immediate action to preserve habitat seems obvious. In the 1959–60 post-hunting season sale of Duck Stamps, only 1,153 stamps were sold up to mid-May 1960. This special sale was held to permit interested citizens to contribute to the essential land acquisition fund. With over two million waterfowl hunters and a much larger group of interested non-hunters, it is apparent that financial support from this special effort was meager. However, public understanding undoubtedly increased somewhat.

Behavioral characteristics of waterfowl help to maintain public apathy. Large concentrations occur during migration and on the wintering grounds. Locally, the birds are abundant. Apparently, what few people realize is that many times they are seeing a large percentage of a given species or manageable flock. Similarly, local shooting success may be high due to exceptional food, water, and hunting conditions. When personal sightseeing and hunting success is high, how many people will purchase an extra Duck Stamp to enlarge the habitat preservation fund? Apparently few.

In addition to supporting programs, the public must clearly recognize the need for changing the broad U.S. Congressional policy encouraging drainage. Technical aids and payments from the government for draining marshes of value to waterfowl should be denied in the Prairie Pothole Region. This action is essential to maintain the type of habitat required to produce a resource that is largely in the public interest.

Because of the magnitude and importance of the breeding habitat and crop depredation problem in Canada, international action is being considered to meet the issues. A Waterfowl Study Committee of the International Association of Game, Fish, and Conservation Commissioners has been evaluating and is continuing to evaluate the need and desirability of establishing an International Waterfowl Advisory Committee or Commission to help resolve the conflicts in land use.

Action on the major waterfowl conservation issues is needed **now.** With proper public support and management, particularly on migration and wintering areas, the numbers of geese, especially Canadas, can very likely be enlarged. Lack of practical solutions to preserve the potholes will result in a reduction in the volume of the duck and coot flight. Extirpation of species is not involved. Rather, the challenge is to maintain a reasonable volume of waterfowl to meet present and expanding future demands of the public.

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ORNITHOLOGICAL LITERATURE

COMPARATIVE BREEDING BEHAVIOR OF FOUR SPECIES OF NORTH AMERICAN HERONS. By Andrew J. Meyerriecks. Publications of the Nuttall Ornithological Club No. 2, 1960: 6 × 9¼ in., viii + 158 pp., 15 pls., 39 figs., 20 tables. Paper, $2.00; cloth, $3.00. (Order from Massachusetts Audubon Society, Drumlin Farm, South Lincoln, Mass.)

This interesting work is concerned primarily with the hostile and sexual displays of the Green Heron (*Butorides virescens*) and the interactions of birds showing these displays during pair formation. Various maintenance activities are also described as a basis for understanding the origin of the sexual and hostile displays. Pairing behavior of the Green Heron is thoroughly documented and much information is condensed into "ethograms." Comparative information on pairing behavior is given in somewhat less detail for the Great Blue and Great White Herons (*Ardea herodias*), the Reddish Egret (*Dichromanassa rufescens*), and the Snowy Egret (*Leucophoyx thula*). In addition, the presence or absence of 61 behavior patterns found in herons is shown in chart form for all North American herons except the bitterns. One of the real values of this chart is its exposure of the many gaps in the knowledge of our common herons. The author includes a discussion of evolutionary trends in heron behavior as related to sociality, polymorphism, sexual dimorphism and pair formation, coloration of soft-parts, and size and activity.

The primary contribution of this paper is the description of displays and pairing behavior of the Green Heron, based on some 3,000 hours of observation. One can only hope that this study will serve as a backbone for further detailed studies of herons throughout the world comparable to the work being done on many species of gulls. Unfortunately there is still no detailed account of the later breeding behavior in the Green Heron.

The pairing of the Green Heron starts with the attraction of a female to the territory of a male. As reflected by a series of displays, some of them mutual, the hostile tendencies in both birds are gradually overcome by sexual tendencies. The territory of the male is gradually reduced to the nest itself, which is at all times the heart of the territory. The female approaches the nest gradually, and the pair bond is established when the female stands on the nest and both birds express their sexual drive through the Stretch Display, Billing, and Feather Nibbling. Meyerriecks has analyzed this stage of the breeding period in detail and with great clarity.

A number of "ethograms" are presented, showing graphically the actions and reactions of two birds for a particular time interval (usually about an hour—almost three hours in one case). One weakness of the ethograms, and of the entire study, is the lack of definite individual or sex recognition, since color banding was not employed. Sexing was based on "observed behavior and soft-part color."

Commenting on the value of behavior studies for systematics, the author states that "when groups of species are closely related, the ethologist usually has little difficulty in determining those displays which are homologous." Homology, of course, is the criterion by which we must judge the degree of relationship, and the difficulties of interpreting similarities of certain behavior patterns cannot be denied. Meyerriecks mentions the physical similarity between the Stiff-necked Upright Display of the Green Heron and the Aggressive Upright Display of the Great Blue Heron. As he points out, these displays are probably of different origins and therefore not homologous, and they serve different functions. Because of the relatively limited number of distinctive positions which a bird can assume, it is not surprising that certain nonhomologous displays would show fortuitous similarities. It is clear that behavior studies must be thorough and critical to prevent misinterpretation.

Behavior patterns, like anatomical structures, show geographic and individual variation which must be known to allow meaningful comparison with other forms. The author should be applauded for describing variability wherever possible. Thus, he shows that the advertising call of the male Green Heron exhibits geographical variation in pitch and pattern, and he gives a quantitative description of individual variability in the Stretch Display. Whether the geographical variation in call is inherited or learned has yet to be determined.

On the basis of comparative behavior Meyerriecks supports the idea that the Great Blue and Great White Herons are conspecific, and, contrary to Bock (Amer. Mus. Nov. No. 1779, 1956), that *Dichromanassa rufescens* and *Leucophoyx thula* are congeneric.

In criticism of this work I feel that, whereas the section on the Green Heron is firmly based on fact, the section on the other three species is based on relatively few observations. The portion on evolutionary trends is highly speculative and its inclusion is not wholly appropriate. This space might better have been used for critical comparison of the behavior of the four species studied. The drawings illustrating displays are adequate but uninspired, and it is disappointing to find that most of the photographs show maintenance activities rather than displays. Finally, the work might better have been entitled "Comparative *Pairing* Behavior of Four Species of North American Herons."—RICHARD L. ZUSI.

A FIELD GUIDE TO THE BIRDS OF TEXAS. By Roger Tory Peterson. Published for the Texas Game and Fish Commission by Houghton Mifflin Company, Boston, 1960: 4½ × 7½ in., xxxii + 304 pp., 60 full-page plates (36 in color), numerous text figures, 2 maps, 13 pages of silhouettes. Available only from the Texas Game and Fish Commission, Austin. $3.00 postpaid.

No longer must resident and visiting bird students in Texas burden themselves with two or three bird guides. This attractive and colorful book, the most recent in the Peterson field guide series, is a welcome addition to the small list of worth-while works on identification of southwestern birds. Covering 542 species, it is almost as valuable to workers in the neighboring states as in Texas. (A hasty check reveals inclusion of all but 15 or 16 of the regularly occurring birds in southwestern New Mexico and southeastern Arizona.) The volume is so superior to anything else currently available that it is already enjoying widespread use by bird students visiting New Mexico from all parts of the country. All Texas bird students of my acquaintance are busily wearing out their copies and have been doing so for several months. The popularity of the new guide is indicated by the following statement in the 2 May 1960 issue of *Time*: "Without advertising, and despite a sales system that seems designed to discourage all but the most determined customers, the Texas *Field Guide* has sold more than 6,000 copies—better than some bestselling novels." Not until the long-awaited revision of Peterson's "Field Guide to Western Birds" is available will field students leave the Texas Guide home on their shelves.

Peterson has once again demonstrated his ability to condense volumes of information into small quarters. The main problem in preparing any field guide is space; but in this small book, only 14 pages longer than his eastern Guide, 487 species are discussed in the main text. Each is given the familiar concise treatment typical of Peterson's other books, with additional brief comments concerning habitat, nest, and eggs. An additional 55 accidental species and two hybrids are described in an appendix. Subspecies are ignored unless two or more distinctive races occur in Texas. In such cases the forms are discussed under a single species heading in the text. Subspecific names on the plates vary slightly; the two figured forms of Rufous-sided Towhees are labelled "Eastern type" and

"Western type"; the races of Gray-headed Junco are termed "*caniceps form*" and "*dorsalis form*"; the two figured Fox Sparrow subspecies are simply designated "Typical form" and "Western form." The text, however, usually names the races occurring in the state.

Vernacular names are those of the AOU Check-list, 5th edition. Earlier "official" names are given in parentheses as are certain other names used in Richard Pough's "Audubon Bird Guides" or by *Audubon Field Notes* for several years but which never had been sanctioned by the AOU. These appear in quotation marks. The family accounts are somewhat longer than those in other Peterson Guides, including brief remarks on food, habits, and the number of species in the world, in North America, and in Texas.

Some of the plates are the same as those in the author's eastern Field Guide (e.g., terns, waders, rails, waterfowl, hawks, shorebirds, owls, spring warblers, and confusing fall warblers). Two-thirds of them, however, are new, and some of these will be used in the new edition of "A Field Guide to Western Birds." Among the 19 wholly new color plates are particularly good illustrations of flycatchers, vireos, thrushes, and sparrows. To my way of thinking the colorful oriole and tanager plate and the plates of the vireos and streaked sparrows are the best. These, and many others, not only are the finest pictures available for identification purposes but are artistically executed despite being field-guide-type profiles.

Reminiscent of the European Field Guide are the small flight pictures of the Mockingbird, Loggerhead Shrike, and Phainopepla (Plate 45). I have noticed one slip of the brush: on Plate 53 the rump of the Red-faced Warbler should be bright white, not gray.

Some persons would perhaps argue that strict accidentals (and even hypotheticals like Anna's, Costa's, and Allen's Hummingbirds) in Texas should not have been figured in color alongside regularly occurring species. However, in each such case the reader is adequately informed in both picture captions and text of the bird's apparent status. With these cautions I believe their inclusion has made the book more useful. Figuring the stragglers and hypotheticals in color has served the additional purpose of allowing the same plates to be used again in the forthcoming edition of the western Field Guide.

The Golden-crowned Warbler is figured in color but other Mexican species hypothetical in Texas, such as the Clay-colored (Gray's) Robin and Ruddy Ground Dove, are not illustrated. These and the other accidentals are, however, carefully discussed in Appendix I, which lists the details of all records "when the existence of a bird in the state list hangs on a hypothetical sight record." It should be noted that Peterson has wisely excluded very unlikely species (Black Catbird, Abert's Towhee, Short-tailed Hawk, and others) which probably have been erroneously assigned to the Texas list. It is barely possible that at least one of the Sulphur-bellied Flycatchers reported from Texas could actually have been the very similar *Myiodynastes maculatus* which occurs regularly in southern Tamaulipas along with *M. luteiventris*. This possibility is not mentioned, and the statement that no other flycatcher has a streaked breast of course applies to the AOU Check-list area only.

Although the book is written in nontechnical language and with emphasis on the ease of distinguishing species in life, Peterson has nevertheless been cautious and helpful in his statements dealing with certain difficult groups. It will be reassuring to many readers who have despaired over melanistic buteos to learn that "even the seasoned expert gives up on some of the birds he sees," that distinguishing the Olivaceous from the Double-crested Cormorant when the two are not together is "one of the *real problems* of Texas field ornithology," that it is impossible to identify all individual juncos, etc.

Probably it is inevitable that a few minor field problems (such as the beginner's difficulty in distinguishing young Black-throated Sparrows from Sage Sparrows in late

summer) would be overlooked or omitted in order to conserve space; but it would be misleading and unfair to dwell on the very few such minor omissions in a volume which covers so much and in such a highly satisfactory manner.

In summary, the book in every way meets the standard of excellence we have learned to expect from Roger Peterson. Any misgivings one may have had about the value of a major field guide to only Texas birds will be dispelled upon using this book in Texas or the adjoining states. It appears to have been a worth-while venture in every respect. —Dale A. Zimmerman.

Zulu Journal: Field Notes of a Naturalist in South Africa. By Raymond B. Cowles. University of California Press, Berkeley and Los Angeles, 1959: 6 × 9¼ in., xiv + 267 pp., photos., map. $6.00.

I cannot praise this book too highly for it is not the usual story of an American naturalist's adventures in a faraway land. Indeed, it is a classic of its kind and should be read by everyone with an interest in the field aspects of biology, in conservation, and in the human problems which beset Africa today.

Dr. Cowles, a Professor of Biology at the University of California in Los Angeles, is a scientist of broad interests with the enviable ability to express himself lucidly. His text is absorbing in content, masterfully composed, and a joy to read. It never strains to be sensational or funny; it is never dependent on pictures, although there are 32 pages of good photographs in the middle of the book.

Born in the Hluhluwe Valley of Natal, South Africa, a son of missionary parents, Dr. Cowles spent his boyhood there and later returned three times, the last in 1953. His many personal impressions and experiences obtained in that country over a span of some fifty years provide the substance of "Zulu Journal." In it he has shifted attention away from the big mammals—so often the dominant elements in accounts of outdoor Africa—and emphasized instead the smaller wildlife. Of these he writes feelingly, with careful attention to form, color, vocal sounds, and behavior. He is constantly heedful of each animal's role in the ecological scheme and has the happy facility of letting the reader share with him the excitement of each observation and discovery. I shall not soon forget his vivid description of the nuptial flight of termites nor his account of how termitaria are utilized by monitor lizards as nesting sites.

There is much about birds that is highly illuminating. This is especially true of the chapter, "Bird Life and the Seasons," which covers a variety of such topics as the parasitic habits of the Lesser Honey Guide, the unique nesting behavior of hornbills, and the clustering of colies and their evident ability to hibernate.

Dr. Cowles is ever mindful of man's relationship to wildlife, both as one element in the fauna and as a potential destroyer, and he voices grave concern lest *Homo sapiens*, through overpopulation and "lack of adequate future subsistence," will bring disaster to both wildlife and himself. The final chapter, "Man," is a penetrating appraisal of Africa's human problems and their impact on that continent's wildlife, today and in the future.

Though Dr. Cowles remarks in his introduction that his book is not a biological treatise, it is nevertheless about biology and beautifully illustrates many a biological principle. Furthermore, it makes Africa seem the challenging place for research that it is and may cause readers to wonder why, to use the author's words, "Europe and its laboratories have an apparently greater appeal for our vacationing sabbatics than Africa with its fascinating possibilities of random discoveries."—Olin Sewall Pettingill, Jr.

WILDLIFE IN AMERICA. By Peter Matthiessen. The Viking Press, New York, 1959: 7 × 10 in., 304 pp., 8 col. pls., 16 bl. & wh. pls., over 100 drawings, 1 map. $10.00.

This handsome volume embodies the most eloquent plea for conservation I have ever read. If it could only become required reading for all Congressmen and state legislators, and all appointive officials empowered to promote conservation, our wildlife—what there is left of it—might still have some chance of survival.

"Wildlife in America" is primarily a historical review of our vertebrate animals in the face of the white man's onslaught from early times to the present. It is not pleasant reading, this story of how one species after another has retreated toward extinction, but it is by no means dull, for the author, a talented novelist, writes with facility, force, and color. While being carefully factual in all matters of history, ecology, and biology, he manages to give a stirring account of the greed and shortsightedness that have caused the decline of so many species and to arouse one's dismay and resentment at the apathy of most public officials and citizens toward corrective measures. In order that the animal subjects about which he writes may not be just so many names, he has cleverly worked in numerous commentaries that give them significance and personality—and at the same time excite the reader's interest and sympathy. Mr. Matthiessen's superb text is supplemented substantially by the illustrations—notably the excellent line drawings (averaging one to every other page) by Bob Hines. Practically all species mentioned are pictured. Several chapters in the book deal at some length with the rise of conservation organizations and their bitter struggles, more often lost than won, to stave off the seemingly inexorable trend of species and their habitats toward destruction.

Of great worth as reference material are two appendices, one listing the vertebrate animals north of Mexico that are rare, declining, and extinct, and the other listing chronologically all legislation affecting North American wildlife.

Besides the more than 100 line drawings, the book has eight color plates showing examples of historic work by wildlife illustrators from Catesby to Fuertes, and 16 plates containing black and white reproductions of photographs and early drawings of American wildlife. These embellishments, together with the splendid format, fine quality of paper, and so on, account for the high cost of the book. I hope that eventually an edition at lower cost will be produced so that the book will enjoy a wider sale and its plea for conservation, consequently, a wider readership.—OLIN SEWALL PETTINGILL, JR.

OUTDOOR REFERENCE GUIDE. Compiled by Amelia Reynolds Long. The Stackpole Company, Harrisburg, Pennsylvania, 1959: 7 × 10¼ in., 288 pp., 24 full-page photos. $7.50.

This is essentially an abridged encyclopedia for outdoorsmen. Different animals, plants, minerals, "natural wonders" (e.g., Mammoth Cave), weather phenomena, geographical features (e.g., quagmire), and terms used in sports are listed in alphabetical order, followed by brief descriptions or explanations in simple language. In many instances some pertinent fact is given to enliven reader interest. The book is more suitable for browsing than for reference, as it does not attempt thorough coverage. For example, it includes only 11 New-world warblers. Sumptuous in size and attractively bound, "Outdoor Reference Guide" should make a decorative addition to one's living room table or fireside book shelf at the summer cottage.—OLIN SEWALL PETTINGILL, JR.

CHECK-LIST AND BIBLIOGRAPHY ON THE OCCURRENCE OF INSECTS IN BIRDS' NESTS. By Ellis A. Hicks. The Iowa State College Press, Ames [1959]: 6 × 9¼ in., 681 pp. $8.50.

This book has two check-lists, one of insects (18 orders) found in birds' nests and one of birds (26 orders) in whose nests insects have been found. Both lists contain many hundreds of references to a 68-page bibliography. There is also an index to taxonomic groups of insects and birds above species.

The work represents an effort by the author "to assort and consolidate information" gathered from publications pertaining to insects and birds. His task has been prodigious for the specialized information needed has been widely scattered in books and journals the world over. Primarily an entomologist, he has nevertheless had to become conversant with ornithology in order to process his data. That the result of his effort will be helpful to entomologists and ornithologists alike, I have no doubt. I only wish that, besides assorting and consolidating his information, he had also been more discriminating.

Unfortunately many of the insects listed as occurring in birds' nest are neither parasitic on birds nor directly associated with their nests. They are simply insects reported from nests—occupied or long since abandoned—that could just as likely have been found in clumps of dead grass, heaps of forest-floor debris, crotches of trees, tree cavities, or countless other situations. To cite one example: under Robin, *Turdus migratorius*, there are listed such free-living insects as thrips, springtails, midges, and asparagus beetles along with numerous insect parasites. No distinction is indicated. It is left to the user of the book to decide or determine which of these insects properly belong in nests.

In the ornithological check-list many insects are listed as found in nests of *undetermined* bird species and, in numerous instances, of *undetermined* genera, families, and orders. I seriously question the worth of this procedure, particularly since it has necessitated many more pages and thus increased the bulk and cost of the work.

The primary usefulness of the book to ornithologists lies in its accumulation of references to some of the more important literature on insects living in birds' nests as parasites or associates.—OLIN SEWALL PETTINGILL, JR.

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SUGGESTIONS TO AUTHORS

Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, and on one side only of good quality white paper. Tables should be typed on separate sheets. Before preparing these, carefully consider whether the material is best presented in tabular form. Where the value of quantitative data can be enhanced by use of appropriate statistical methods, these should be used. Follow the AOU Check-list (Fifth Edition, 1957) insofar as scientific names of United States and Canadian birds are concerned unless a satisfactory explanation is offered for doing otherwise. Use species names (binomials) unless specimens have actually been handled and subspecifically identified. Summaries of major papers should be brief but quotable. Where fewer than five papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "Style Manual for Biological Journals" (1960. AIBS). Photographs for illustrations should be sharp, have good contrast, and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Authors are requested to return proof promptly. Extensive alterations in copy after the type has been set must be charged to the author.

A WORD TO MEMBERS

The Wilson Bulletin is not as large as we want it to be. It will become larger as funds for publication increase. The Society loses money, and the size of the *Bulletin* is cut down accordingly, each time a member fails to pay dues and is put on the "suspended list." Postage is used in notifying the printer of this suspension. More postage is used in notifying the member and urging him to pay his dues. When he does finally pay he must be reinstated in the mailing list and there is a printer's charge for this service. The *Bulletin* will become larger if members will make a point of paying their dues promptly.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, Merrill Wood, Dept. of Zoology and Entomology, Frear Laboratory, Pennsylvania State University, University Park, Pennsylvania. He will notify the printer.

1961 ANNUAL MEETING

The 1961 meeting of the Wilson Ornithological Society will be held from Thursday to Sunday, 8–11 June, at Huntsville, Ontario, Canada. The meetings will be held at Britannia Lodge, in the Muskoka District, under the sponsorship of the Federation of Ontario Naturalists, the Audubon Society of Canada, and the Royal Ontario Museum.

This will be the first annual meeting of the Society held in Canada.

The program plans of Dr. Murray Speirs and his colleagues include a field trip at night to hear wolves howl in response to a recording. Roger Tory Peterson, Second Vice-president of the Wilson Society, will show for the first time in North America his 30-minute film on storks of the world.

More detailed program plans and information regarding best routes, accommodations, etc., will be mailed to members later. Others may receive this material by writing to the Secretary of the Society: Mr. Aaron M. Bagg, Farm Street, Dover, Massachusetts.